Plant and Soil
Water Relationships

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Plant and Soil Water Relationships

By

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PLANT AND SOIL
WATER RELATIONSHIPS

To

EDGAR N. TRANSEAU

Who first directed my attention to the field
of plant-water relations

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PREFACE

This book is intended for teachers, investigators, and students in both the basic and the applied plant sciences. It should be especially useful to botanists, agronomists, foresters, horticulturists, and soil scientists who are interested in plant-water relations. An attempt has been made to present the fundamental facts underlying the various phenomena in relatively simple terms, such as will be intelligible to workers in all fields of plant science. If, as a result, the treatment of certain phenomena seems inadequate to specialists in certain fields, they should remember that this book was written not for specialists in plant and soil water relations, but for those plant scientists who need to have a good general understanding of the field.

Considerable attention has been given to the application of the basic physical and physiological principles in explaining plant growth. While knowledge of plant processes has an intrinsic scientific value, it attains maximum usefulness only when it is related to the growth behavior of plants. Investigations in the various fields of applied plant science cannot be very productive unless they are based on a thorough understanding of the fundamental principles involved. It is hoped that this book will assist plant scientists to understand better the principles governing plant and soil-water relations and to see how this knowledge can be used to solve problems of plant growth.

The selection of material for this book was based on the author's experience during a number of years of research on the absorption of water by plants. It was found that the absorption of water could not be treated as an independent process but had to be considered in relation to various other processes and conditions. The rates of absorption

and of transpiration are closely related, and together they control the internal water balance of the plant. The rate of absorption is controlled by both plant and environmental factors. The principal plant factors are the rate of water loss and the extent and efficiency of the root system. Important environmental factors are the amount of readily available soil moisture, concentration of the soil solution, soil temperature, and soil aeration. A complete survey of the various factors involved in water absorption requires consideration of the principles governing the availability of soil moisture, the structure of roots and factors effecting development of root systems, the water relations of plant cells and tissues, the nature of the absorption process, and the relation between water and solute absorption. The discussion of these diverse topics has been integrated in terms of their relations to the intake of water. Although transpiration, the ascent of sap, and drought resistance are also important aspects of plant-water relations, they are not discussed because they are not directly related to water absorption.

Because so many papers have been published on water relations, it was impossible to cite them all; therefore numerous good papers were omitted. Enough have been cited on each topic, however, to introduce the reader to the literature of that particular field. In addition to summarizing the literature in several related fields, the author has attempted to evaluate it and draw general conclusions from it. When differences of opinion exist, the author has indicated what seems to him to be the most logical conclusions, but he realizes that some readers will probably disagree with certain of these conclusions. In some instances our knowledge is still too limited to permit definite conclusions, and there is need for further research on many problems. As more is learned concerning various processes, it may become necessary to modify or even abandon some of our present beliefs. It is well to remember that many so-called scientific explanations are true only in the sense

that they represent the best or the most logical conclusions that can be drawn from our present information, and that the acquisition of additional information sometimes requires us to revise our conclusions. Plant physiology, like other branches of science, is continually progressing; therefore views that seem well supported today may become untenable tomorrow as the result of further research.

The author is greatly indebted to various colleagues and friends for their many valuable suggestions. The entire manuscript was read by Ruth M. Addoms and L. E. Anderson of the author's department and by D. B. Anderson of the College of Agriculture and Engineering of the University of North Carolina. Certain chapters were read by H. S. Perry of the author's department and by H. E. Hayward, L. A. Richards, and C. H. Wadleigh of the U.S. Regional Salinity Laboratory, Riverside, California. The manuscript has undergone extensive revision since it was reviewed by these persons; hence they should not be held responsible for any errors that may still exist. The author will be glad to have suggestions from readers concerning corrections and improvements.

Grateful acknowledgment is also made of the receipt of a number of grants from the Research Council of Duke University. These grants have aided the author in his research on plant water relations and contributed both indirectly and directly to the preparation of this manuscript.

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CHAPTER 1

HISTORICAL INTRODUCTION

The absorption of water and solutes from the soil seems to have been the first physiological process to receive the attention of early writers on botanical subjects. A review of the development of our knowledge concerning the absorption of water by plants is therefore essentially a historical review of the early development of plant physiology. This early interest in absorption and the movement of sap in plants was a natural result of the general acceptance of Aristotle's theory of plant nutrition.

Aristotle's Influence

According to Aristotle, plant foods are complex substances which have been so prepared in the soil that they can be absorbed and used by the plant without any changes, hence without the necessity of excreting any wastes or by-products, as do animals. Nutrition of the plant was supposed to be controlled by its soul, or vital principle, which permits each kind of plant to absorb only the kinds of food proper for its growth. Aristotle's theory of plant nutrition was not even seriously questioned until the seventeenth century and was generally accepted until the eighteenth century. Indeed if one can judge from the prevalence of articles and advertising extolling the merits of "plant foods," it is still the generally accepted view of the public. In fact the terminology has not disappeared entirely from scientific circles, as is evidenced by the appearance a few years ago of an excellent book on mineral deficiencies of crop plants, in the title of which the word "hunger" appeared. Another example of the survival of this antiquated terminology is use

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of the term "feeder roots" with reference to the absorbing roots of plants.

The earliest known attempt to explain the absorption process was made by Andrea Cesalpino (1519–1603), an Italian physician and herbalist, in his "De plantis," published in Florence in 1583. He of course accepted Aristotle's theory that plants absorb their food in solution from the soil. Since plants, unlike animals, have no sense perception, he reasoned that they cannot seek food in the manner of animals but must absorb moisture by some special method of their own. After considering and rejecting magnetism and suction as possible agencies, Cesalpino decided that the roots absorb liquid in the same manner as a piece of linen or a sponge. This explanation of absorption as being caused by what we now term capillarity must have been one of the first attempts to explain a plant process in terms of purely physical phenomena.

Questioners of Aristotle

A few decades later, Joachim Jung (1587–1657) attacked some of Aristotle's basic concepts concerning plants. He denied that plants have souls which control their nutrition and enable them to distinguish harmful from useful foods but suggested that possibly the pores of roots are so constructed that some substances can enter, while others cannot. This is perhaps the earliest suggestion of the existence of differentially permeable membranes in plants. Jung questioned whether plants can absorb only useful substances and suggested that they probably excrete waste materials. According to Sachs (1875), Jung stated that possibly a large part of the juices of plants escape by imperceptible evaporation, as in animals. This might be regarded as an allusion to transpiration, though there is no evidence that Jung actually observed the loss of water from plants. About the same time, J. B. van Helmont (1577–1644) attacked the Aristotelean doctrine of plant nutrition even more effectively. He grew a willow tree for 5 years

in a covered pot of soil to which nothing was added but water, and at the end of this period he found that the willow tree had increased 164 lb. in weight, while the dry weight of the soil had decreased only 2 oz. In view of the general state of knowledge at that time, it is not surprising that van Helmont concluded that plants use water as food. Apparently, however, he did not propose any theory concerning the manner in which water was absorbed or incorporated into plant tissue.

Another person who questioned the prevalent doctrines was the French scientist Edmé Mariotte (*ca.* 1620–1684). According to Sachs, Mariotte in a long letter to a friend, in 1679, summarized current views on plant physiology and denied that plants have a soul, or vital principle. He believed that plants produce their own distinctive substances, or foods, from materials absorbed from the soil rather than absorbing them ready for use, as had been claimed by Aristotle. Among Mariotte's arguments to support this view were the facts that thousands of different kinds of plants can be grown on the same soil and that an edible variety of pear grafted on a wild pear produces good fruit on the graft from the same sap which produces worthless fruit on the wild stock. Mariotte observed the occurrence of sap pressure in plants and concluded that it was caused by some device in the roots which permitted the entrance of water but prevented its exit. He believed sap pressure to be responsible for growth, causing the expansion of roots, branches, and leaves.

The Circulation of Sap

Harvey's account of the circulation of blood, published in 1628, increased interest in the movement of sap in plants. Scientists of that day were much inclined to draw analogies between the anatomy and the physiology of plants and of animals; hence they expected to find plant sap circulating in the same manner as the blood circulates in animals. Christopher Merret (1664), an Englishman, and Johann

Daniel Major (1665), a German, claimed to have observed such circulation, and this opinion was commonly held for more than a century, being defended by Thomas Knight as late as the beginning of the nineteenth century. Papers on the movement of sap were presented before the Royal Society of London by Beale, Lister, Ray, Tonge, and Willughby in the period from 1668 to 1671, and Ray and Willughby were asked by the Royal Society to determine whether sap circulates in plants as blood does in animals. They carried out some experiments from which it was concluded that there was both ascent and descent, as well as lateral movement; but they did not commit themselves as to whether or not there was true circulation. They decided that water could move downward as well as upward in the wood because when stems bent over and rooted at their tips, they could then be cut off and grown into new plants. This proved the absence of any sort of valves in the water-conducting system. Although Ray is chiefly known for his taxonomic work, he seems also to have done some of the first experimental work on plants in England. Interesting as this early work is, it contributed little of lasting importance.

Grew and Malpighi

The outstanding contributions of the seventeenth century to the knowledge of plants were made by Nehemiah Grew and Marcello Malpighi. Grew's first paper, which appeared in 1671, was followed by a summary of his work, "The Anatomy of Plants," in 1682. Malpighi published "Anatome plantarum" in 1675. While their studies were chiefly anatomical, both men were interested in plant processes, and Green (1914) states that Grew was primarily a physiologist who studied anatomy in the hope of obtaining a better understanding of plant processes.

Grew apparently thought that the roots absorb by capillarity and that after the pith and parenchyma cells become turgid they force water into the vessels and press on them so that if they are cut, sap flows out. He further believed

that since cut stems and branches bleed at both upper and lower ends, there could be no valves in the conducting system. According to Grew, after the sap is forced into the vessels, it rises by capillarity as high as the diameter of the vessels permit; it is then absorbed by adjacent parenchyma cells and again forced into the vessels, to rise further by capillarity. This bears some resemblance to the theory advanced by Godlewski in 1884. Grew believed that sap rises in the pith, wood, and bark—in the pith only during the first year, in the wood of only certain species, and then only in the spring. "For the greater part of the year, it riseth in the Barque." According to this theory, the vessels of the wood are filled with air or water vapor most of the year. Malpighi also believed the vessels to be filled with air and to exhibit peristaltic movements, and he named these vessels tracheae. Grew distinguished between bleeding, such as that of the vine in the spring, and exudation from the inner bark observed at other seasons, stating that "there is as much difference between Bleeding in a Vine, or the Rising of the Sap in any other Tree in March and July, as there is between Salivation and an Haemorrhage." In discussing the functions of leaves, he wrote: "Now the Sap having a free reception into the leaves, it still gives way to the next succeeding in the Branches and Trunk, and the voyding of the sap in these, for the mounting of that in the Root, and ingress of that in the ground." It might be supposed from this that Grew understood that the loss of water from the leaves causes the intake of water by the roots. While it is interesting to reinterpret these old writings in terms of modern theories, such supposition is somewhat dangerous, since we doubtless often credit the writers with a much more precise meaning than they intended. Both Grew and Malpighi believed that the sap undergoes some change in the leaves which increases its value in nutrition, after which it moves to the fruits or downward to the roots. Malpighi observed stomates on the leaves and is said to have understood their function.

These men were careful workers whose observations in plant anatomy were not equaled for more than a century, but they were not very successful in interpreting their observations in terms of functions. This may be attributed partly to the fact that they were content to speculate concerning physiological processes rather than to attempt studying them experimentally.

Stephen Hales

The first truly quantitative experiments on plant-water relations were those of Stephen Hales (1677–1761), described in his "Vegetable Staticks" (1727), a book which ought to be read by every plant physiologist. Not only is Hales revered by plant physiologists as the first careful investigator of plant processes, but he is also highly regarded by animal physiologists for his pioneer measurements of blood pressure, published in his "Haemostaticks" (1733). Hales was not only physiologist, clergyman, and humanitarian but also a very practical man, who believed that an understanding of plant processes would be useful in growing plants. In the conclusion to "Vegetable Staticks," after discussing some applications of his experiments he makes the following statement:

"I have here, and as occasion offered under several of the foregoing Experiments, only touched upon a few of the most obvious instances, wherein these kind of researches may possibly be of service in giving us useful hints in the culture of plants: Tho' I am very sensible, that it is from long experience chiefly that we are to expect the most certain rules of practice, yet it is withal to be remembered, that the likeliest method to enable us to make the most judicious observations, and to put us upon the most probable means of improving any art, is to get the best insight we can into the nature and properties of those things which we are desirous to cultivate and improve."

The reason why Hales's work was so much better than any

previously done is made clear by a quotation from his introduction:

"And since we are assured that the all wise Creator has observed the most exact proportions, *of number, weight and measure,* in the make of all things; the most likely way therefore, to get any insight into the nature of those parts of the creation, which come within our observation, must in all reason be to number, weigh and measure." And number, weigh, and measure he did, in a manner never previously attempted on plant processes.

Influenced, no doubt, by his work on blood in animals, Hales placed great emphasis on the importance of sap in plants, writing:

"And since in vegetables, their growth and the preservation of their vegetable life is promoted and maintained, as in animals, by the very plentiful and regular motion of their fluids, which are the vehicles ordained by nature, to carry proper nutriment to every part; it is therefore reasonable to hope, that in them also, by the same method of inquiry, considerable discoveries may in time be made, there being, in many respects, a great analogy between plants and animals."

As a result of this view, most of his attention was given to studies of the absorption and translocation of water. Transpiration, or (as it was then termed) perspiration, of various species of potted plants was measured by weighing the pots. The soil surface was covered, and corrections were made for evaporation from the surfaces of the pots. Root and leaf surfaces of a sunflower and of a cabbage plant were determined by measuring representative samples and calculating the totals. This was an early use of the sampling technique, and the results are the first known measurements of root systems and leaf areas. Hales measured transpiration rates of potted grapevine, apple, lemon, and mint in his garden; and the famous gardener Philip Miller, of Chelsea Garden, measured the transpiration rates of aloe, banana, and apple in his hothouses, where the effects of temperature

could be observed more easily. Hales observed that the transpiration rate varied with the species, time of day, temperature, and brightness of sun, which is in accord with modern findings. Samples of water vapor were collected in glass vessels placed around transpiring branches, and it was decided that the condensed liquid probably was not pure water because when allowed to stand, it began to stink sooner than water. Absorption by cut branches was measured and the force with which they absorbed water was demonstrated by the fact that a transpiring branch absorbed water several times as rapidly as it could be forced through the branch by a column of water 7 ft. high. Finding that no water would exude from the upper end of cut stems, although the lower ends were immersed in water, he decided: "These three last experiments all show, that tho' the capillary sap vessels imbibe moisture plentifully; yet they have little power to protrude it farther, without the assistance of the perspiring leaves, which do greatly promote its progress."

The amount of water held in a cubic foot of soil was measured, and the amount lost by evaporation was compared with that supplied by rainfall. Hales then described a series of experiments intended to determine the force with which plants absorb water. This was done by fastening glass tubes to the cut ends of attached roots and branches, filling the tubes with water, and dipping the open ends into vessels of mercury. As the root or the branch absorbed water, the mercury rose in the attached tube. The rise was greatest on sunny days and least at night, and no rise occurred if the leaves were removed. Water was even absorbed with considerable force through the upper ends of bent branches, proving that it could move in either direction in the conducting system. By removing rings of bark, Hales demonstrated that water rises through the wood rather than through the bark, but he apparently believed that considerable water moved upward between the wood and the bark and that removal of or injury to the bark, therefore, de-

creased the supply of sap to tissue above the girdle or the injury. He also observed the swelling of the bark above girdles but did not satisfactorily explain it.

Hales measured the pressure with which sap exuded from cut stems of various species by means of mercury manometers, observing a maximum pressure equal to 43 ft. 3.3 in. of water on a grapevine. He observed the effects of variations in temperature, moisture, and time of day, and found that exudation occurred only in the spring, water being absorbed by cut surfaces at other seasons instead of exuding. These variations were explained as follows: "But by many observations . . . we find the sap in the tubes constantly subsided as the warmth came on towards the middle of the day, and fastest in the greatest heat of the day. Hence we may reasonably conclude, (considering the great perspirations of trees, shown in the first chapter) that the fall of the sap, in these sap gages, in the middle of the day, especially in the warmer days, is owing to the then greater perspiration of the branches, which perspiration decreases, as the heat decreases toward evening, and probably wholly ceases when the dews fall.

"But when towards the latter end of *April,* the spring advances, and many young shoots are come forth, and the surfaces of the Vine is greatly increased, and enlarged by the expansion of several leaves; whereby the perspiration is much increased, and the sap more plentifully exhausted, it then ceases to flow in a visible manner till the return of the following spring.

"And as in the Vine, so is the case the same in all the bleeding trees, which cease bleeding as soon as the young leaves begin to expand enough, to perspire plentifully, and to draw off the redundant sap."

In another place he writes, "From these Experiments, I say, it seems evident, that the capillary sap vessels, out of the bleeding season, have little power to protrude sap in any plenty beyond their orifices; but as any sap is evaporated off, they can by their strong attraction (assisted by the ge-

nial warmth of the sun) supply the great quantities of sap drawn off by perspiration."

Apparently Hales understood that there is a close relation between absorption and transpiration and believed that transpiration itself sets in motion the forces causing the absorption of water and its ascent to the leaves, a view quite in accordance with those held today. Apparently absorption by the roots was regarded as a physical process, but no real attempt was made to explain how the root pressures he observed were developed. There is some indication that he regarded the roots as differentially permeable, for he wrote, "I shall begin with an experiment upon roots, which nature has providently taken care to cover with a very fine thick strainer; that nothing shall be admitted into them, but what can readily be carryed off by perspiration, vegetables having no other provision for discharging their recrement."

The common belief that sap circulates in trees as does blood in animals was carefully investigated. On this question Hales wrote as follows:

"Upon the whole, I think we have, from these experiments and observations, sufficient ground to believe that there is no circulation of the sap in vegetables; not withstanding many ingenious persons have been induced to think there was, from several curious observations and experiments, which evidently prove, that the sap does in some measure recede from the top towards the lower parts of plants, whence they were with good probability of reason induced to think that the sap circulated." He did demonstrate that lateral movement of sap occurs where the direct upward path has been interrupted by deep cuts into the center of the stem, but he could find no evidence of downward movement.

Hales's ideas concerning plant nutrition probably were no better than those of Grew and Malpighi. He seems to have regarded the chief function of the leaves as the attraction of sap to the growing regions, although he believed that they

absorbed air and suggested that the light striking the leaves might also contribute to the plant in some manner.

A Century of Limited Progress

A century passed before another contribution as valuable as that of Hales was made to the problem of plant-water relations. Meantime Ingen-Housz, Senebier, and particularly De Saussure developed the field of plant nutrition. In the course of his studies on mineral nutrition, De Saussure (1804) found that the absorption of minerals was not proportional to the absorption of water. Furthermore, he observed that different substances were not absorbed in the same proportions in which they occurred in the soil and that useless and even poisonous substances, as well as useful substances, were absorbed. According to Sachs, Senebier also observed that the rate of transpiration of plants was affected by the presence of various solutes in the soil solution. This early work was generally forgotten or overlooked.

During the first quarter of the nineteenth century, little progress was made in plant physiology. Sachs (1875) attributed this lack of progress to two factors. One was the tendency to explain all phenomena not otherwise easily explained as caused by some vital force, which according to the Aristotelean doctrine was supposed to control plant processes. Another cause was the neglect of the contributions of such competent investigators as Grew, Malpighi, Hales, and even De Saussure. A third cause may have been the lack of professional plant physiologists who had time to concentrate on these problems. The early physiological work was done chiefly by men whose primary interests were in other fields. Hales was a clergyman, De Saussure had numerous other interests, and De Candolle was primarily a taxonomist. Sachs was the first professional botanist to concentrate his major attention on plant physiology, and there were relatively few professional plant physiologists until after the beginning of the present century.

De Candolle's Spongiole Theory

An example of the unsatisfactory state of botanical knowledge at that time was the wide acceptance of the spongiole theory of A. P. de Candolle (1832). De Candolle apparently mistook the root caps for contractile absorbing organs, and this view was widely accepted for some years, though careful examination of the root tips ought to have revealed its improbability. His rather confused views are indicated by the following quotation:

"The spongioles of the roots, being actively contractile and aided by the capillarity and hygroscopic qualities of their tissues, suck in the water that surrounds them together with the saline organic or gaseous substances with which it is laden. By the operation of an activity which is manifested principally in the contractility of the cells and perhaps also of the vessels, and is maintained by the hygroscopic character and capillarity of the tissue of the plant and also by the interspaces produced by the exspiration of air and by other causes, the water sucked in by the roots is conducted through the wood and especially in the intercellular passages to the leaf-like parts, being attracted in a vertical direction by the leaves and in a lateral direction by the cellular envelope (cortical parenchyma) at every period of the year, but chiefly in the spring; a considerable part of it is exhaled all day long through the stomata into the outer air in the form of pure water, leaving in the organs in which the evaporation takes place all the saline, and especially all the mineral particles which it contained." [1]

It seems that Hales had a clearer understanding of the forces operating to cause the absorption of water and its ascent in stems than did De Candolle.

Dutrochet's Osmotic Theory

Henri Joachim Dutrochet (1776–1847) contributed more to plant physiology and particularly to an understanding of

[1] J. von Sachs, "History of Botany," p. 517, English trans., Oxford University Press, New York, 1890.

plant-water relations than did any other worker in the first half of the nineteenth century. His observations on the discharge of spores from sporangia and similar phenomena led him to formulate as early as 1826 a theory of osmosis, which he gradually extended to explain a wide variety of plant phenomena. This theory dealt a hard blow to the doctrine of vital forces, because many processes that were previously explained as manifestations of a vital force could now be explained in terms of a purely physical process, osmosis. Dutrochet differentiated between the rise of sap in transpiring plants and the bleeding from detopped roots, the latter being caused by impulsion, the former by attraction. He believed that sap pressure and bleeding were caused by osmosis, the roots behaving like osmometers. Sap was supposed to rise in stems by osmosis from cell to cell, but he does not seem to have had a clear notion of how this could occur. Although Dutrochet first developed the concept of osmosis and related it to the absorption of water and salts, his ideas on the subject were very different from those held today. He seems to have had no real comprehension of the functioning of the differentially permeable membranes with which he was working. He believed, for example, that entrance of water was always accompanied by the exit of a related quantity of solutes. This seems to have been, at least in part, the basis for development of an extensive interest in root secretions. Dutrochet's theories were inadequate to explain how different salts enter plants in different quantities, though De Saussure had already proposed a theory of differential permeability to explain this. Dutrochet did good work in other fields of plant physiology, especially respiration. His "Mémoires pour servir à l'histoire anatomique et physiologique des végétaux et des animaux" (1837) was one of the best physiological publications prior to Sachs's text.

Laying the Foundation for Modern Concepts

After the middle of the nineteenth century, rapid progress was made in the fields of chemistry and physics. Thus some of the basic information so badly needed for a satisfactory interpretation of physiological phenomena was provided. Graham's studies resulted in the distinction between colloidal and crystalloidal materials (1862) and he also studied osmosis. Traube (1867) applied Graham's concepts to the study of cells and demonstrated that cell membranes are largely colloidal in nature. He experimented with model cells and proposed a sieve theory to explain differential permeability. His work disposed of Dutrochet's idea that endosmosis must be accompanied by exosmosis.

Pfeffer (1877) made noteworthy contributions to the understanding of osmotic phenomena, especially the nature of differentially permeable membranes. He, like Traube, held to a sieve theory of differential permeability but believed that the protoplasm could regulate the character of the membrane and hence its permeability. The more modern view that the protoplasm can actually bring about the intake of salts apparently was first proposed by Reid (1890). De Vries (1877) studied plasmolysis and first explained the conditions necessary for the development of turgidity in cells. Incidental to these studies was his establishing of a relationship between molecular weight and osmotic pressure. The work of Pfeffer and De Vries was of great interest in chemistry as well as in physiology. The data of De Vries, for example, were used by Arrhenius to support his ionization theory.

In the present century, outstanding contributions to our knowledge of cell-water relations were made by Ursprung (1929), Thoday (1918), and Blackman (1921). These investigators showed that the movement of water is not necessarily along gradients of increasing osmotic pressure, but rather along gradients of absorbing power, variously termed by different writers as suction force, suction tension, diffu-

sion pressure deficit, etc. The term "diffusion pressure deficit" is defined in Chap. 2, and more extensive discussions of the modern terminology of cell-water relations can be found in Crafts, Currier, and Stocking (1949), and in Meyer (1945).

Modern plant physiology is often said to have begun about 1860 with the work of Sachs. This is certainly true of water relations, for Sachs investigated almost every aspect of this problem. He made some of the earliest investigations of soil moisture, soil temperature, and soil aeration in respect to absorption and the growth of roots. He decided that only the water occurring as films around the soil particles is useful to plants and that the accumulation of water in the spaces between the particles is harmful because it decreases the supply of oxygen to the roots. His studies showed that absorption occurs in the root-hair zone instead of in the region of the root cap, as stated in the long-held spongiole theory of De Candolle. Sachs also determined that different soil types hold different quantities of available water—a clay soil, for example, containing much more than does a sandy soil. His work led him to consider the mechanism responsible for the development of sap pressure or, as he first termed it, root pressure. This he attributed to the osmotic activity of the root cells, an inward flow of water occurring because the membranes on the outer surfaces of the cells of the roots are less permeable than those on the inner surfaces. Later he showed that the absorption of water and the loss of water in transpiration are intimately connected, the loss of water producing the pull responsible for the ascent of sap, root pressure being of no importance in supplying water to transpiring plants. Sachs mistakenly believed that the water rises in the walls of the xylem elements, instead of in the lumina, but this error was soon corrected by Elving, Vesque, Strasburger, and others, who showed that blocking the lumina of the xylem prevents the ascent of sap.

During the latter part of the nineteenth century, numer-

ous other papers were published on the osmotic relations of cells and tissues, root pressure, effects of temperature and salts on water intake, and other aspects of the absorption problem. Most of this work is rather specialized and will be discussed later under various special topics. A fuller appreciation of the background from which modern concepts of plant-water relations have developed can best be obtained by reading such textbooks of plant physiology as those by Sachs (1882), Vines (1886), and Pfeffer (1897).

Changing Viewpoints

This review of the history of plant-water relations shows that the viewpoint in this field has undergone changes similar to those which have occurred in other fields of biology. Until early in the nineteenth century, most explanations of biological phenomena were vitalistic in nature. Although the vitalistic viewpoint survived until the end of the nineteenth century in the theory that water is pumped up the stems of plants by living cells, it had begun to be abandoned in the first half of the century. The discovery of osmosis dealt vitalism a heavy blow because it provided a physical explanation for many processes previously regarded as manifestations of a vital force inherent in living organisms. As vitalism was replaced by a mechanistic viewpoint, it began to be assumed that all plant processes could be explained in terms of the chemical and physical processes of the cells. This viewpoint was successfully extended by the research of Traube, Pfeffer, De Vries, and others.

In recent years it has become apparent that the intake of water and solutes cannot be explained solely in terms of the chemical and physical processes of individual cells, for these processes are at least partly controlled by the organism as a whole. This view probably was foreshadowed by the observations of Sachs and Strasburger that the rate of water intake through the roots is determined by the rate of transpiration. It has been made clearer by recent research, which has shown that the intake of solutes by root cells depends in

part on the metabolism of the shoots. The recent revival of the belief that nonosmotic forces are involved in water intake by plant tissues is in opposition to the century-old belief that cell-water relations can be explained as simple osmotic phenomena. Abandonment of the view that mineral absorption by plants can be explained as a physical diffusion process is another example of this shift in viewpoint. It is interesting to note that August Krogh (1946a), the well-known Danish physiologist, describes himself as a vitalist. While he believes that living organisms operate under the laws of chemistry and physics, he feels that many phenomena still defy explanation by the application of those laws.

Consideration of these shifts in viewpoint during the past century should make us cautious about ridiculing some of the apparently erroneous views held a century ago. It may be that some of the most generally accepted of our present-day views may seem equally ridiculous a century hence.

CHAPTER 2

SOIL-MOISTURE RELATIONS

Before studying the absorption of water by plants, one must understand how soil characteristics control the availability of soil moisture.

The Soil

Soil is a complex system consisting of varying proportions of four principal components: rock particles, organic matter, the water and solutes comprising the soil solution, and air. While the amounts of rock particles and organic matter vary but little in a given soil, the amount of water fluctuates over a considerable range, and the amount of air varies approximately inversely with the water content. In addition to the four components just named, soil usually contains numerous living organisms, such as bacteria, fungi, algae, protozoa, insects, earthworms, and small animals, which may directly or indirectly affect plant development. The burrows of earthworms and of small animals, for example, provide passageways that facilitate the downward percolation of water through relatively impermeable soil strata.

The characteristics of a soil depend chiefly on the texture or the size of mineral particles, on the structure or the manner in which these particles are arranged, on the kind of clay minerals present and the kind and amount of exchangeable ions adsorbed upon them, and on the amount of organic matter incorporated with the mineral matter.

Soil Texture. On the basis of texture, soils are usually classified as gravel, sand, loam, silt, or clay, with various intergradations such as sandy loam, silt loam, and clay loam. Silt is intermediate in properties between sand and clay, and

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the proportion of silt present has important effects on soil properties. Soils are classified by the Soil Survey Division of the U.S. Department of Agriculture according to the percentages of sand, silt, and clay present (see Lyon and Buckman, 1943, Fig. 9, page 48). More detailed discussions can be found in soils texts such as Baver (1948), Keen (1931), Lyon and Buckman (1943), and Russell (1937).

Table 1. Classification of Soil Particles According to System of International Society of Soil Science, and Mechanical Analysis of Three Soils *

Fraction	Diameter, millimeters	Sandy loam, per cent	Loam, per cent	Heavy clay, per cent
Coarse sand............	2.00–0.20	66.6	27.1	0.9
Fine sand..............	0.20–0.02	17.8	30.3	7.1
Silt............	0.02–0.002	5.6	20.2	21.4
Clay.................	Below 0.002	8.5	19.3	65.8

* From Lyon and Buckman, 4th ed., p. 43.

Table 1 gives examples of the classification of soil according to particle size. The least complex soil is a sand, which by definition is less than 20 per cent silt and clay and is composed largely of simple rock particles of comparatively large size. Such a soil forms a relatively simple capillary system, with large pores, or air spaces, which ensure good aeration and free movement of gravitational water. Sandy soils are relatively inert, both chemically and physically, are quite loose and noncohesive, and have a very low water-holding capacity.

Clay soils are at the other extreme with reference to size of particles, since they are 30 per cent or more clay particles, most of them of colloidal or near-colloidal dimensions. These particles are usually aggregated in complex granules, which swell and become sticky when wetted. Because of the large proportion of particles of colloidal size in clay, water

and minerals are held in much larger quantities and in a more complex manner than they are in sand. Most soil owes much of its chemical and physical properties to the fraction of clay that it contains. The clay particles, because they are flat and platelike, possess not only the maximum external surface, but also very high cohesive forces. They are usually negatively charged and carry a shell of cations and associated water molecules. The surface possessed by even a small volume of such particles is tremendous. A cubical sand grain 1 mm. on the edge has a surface of only 6 sq. mm.; but if it is divided into particles of colloidal size, 0.1 micron on the edge, the total surface resulting would be 60,000 sq. mm. Because of their platelike shape, clay particles have much greater surfaces than do cubes or spheres of similar size. These extensive surfaces enable clay soils to hold much more water than sandy soils can hold; but since the pores of clay soils are much smaller, gravitational water drains off more slowly, so that these soils are sometimes poorly aerated. Lyon and Buckman (3d ed., page 46) estimated that an acre furrow slice (1 acre in area and 6.6 in. deep) of sand contains 5,000 acres of surface; an acre of silt contains 50,000 acres of surface; and an acre of clay, 500,000 acres of surface.

Loam soils contain more or less equal amounts of clay—or clay and silt—and of sand; therefore they have properties which are intermediate between those of clay and those of sand. Such soils are most favorable for plant growth because they hold more available water than sand does, and because they are better aerated and easier to work than clay is.

Soil Structure. The arrangement of soil particles—soil structure—is important because of its relation to pore size. Soil porosity refers to the portion of the soil volume occupied by air and water. It usually amounts to about half of the volume, generally comprising somewhat less than 50 per cent of the total volume in sand and somewhat more than 50 per cent in clay. Veihmeyer (1935), however, after

summarizing opinions of a number of workers, concluded that it is unsafe to generalize concerning soil texture and porosity because certain beach sands were reported to have about the same porosity as some clays. The total pore space is not so important as is the size of the pores. That portion of the pore space composed of large pores (macropores), from which water usually drains by gravity and which is therefore normally filled with air, is termed the noncapillary porosity, to distinguish it from that part of the pore space which is normally filled with capillary water. The large noncapillary porosity of sandy soils results in better drainage and aeration, but it also results in a lower water-holding capacity than that of clay soils, which have a large proportion of small capillary pores. Baver (1948) states that an ideal soil has the pore space about equally divided between large and small, or noncapillary and capillary, pores. Such a soil has enough large pores to permit adequate drainage and aeration and enough small pores to give adequate water-holding capacity.

Pore-space relationships of two dissimilar soils are shown in Fig. 1. In clay, treatments tending to promote granulation will develop larger pores, and the result will be a more favorable medium for root growth. Some clays swell excessively when wetted, decreasing the amount of pore space and producing a very poorly aerated, unsatisfactory environment for roots. It seems to be generally agreed that the dense mat of roots produced by grass sod promotes granulation and good soil structure, while cultivation usually brings about the opposite effect (Baver, 1948; Bradfield, 1931; Jacks, 1944). The direct effect of root penetration through the soil, followed by their death and decay, is to open up numerous channels and thus materially to increase soil porosity and the penetration of air and water. Earthworm activity has similar effects.

Soil structure is affected also by the kinds of cations present. According to Veihmeyer (1936) there is evidence from laboratory experiments that such properties as moisture

equivalent, deflocculation, hardness of crumbs, and cohesiveness are increased by the substitution of sodium or potassium ions in the exchange complex and are decreased by the substitution of calcium or hydrogen ions. Most investigators seem to think that these results will apply to field
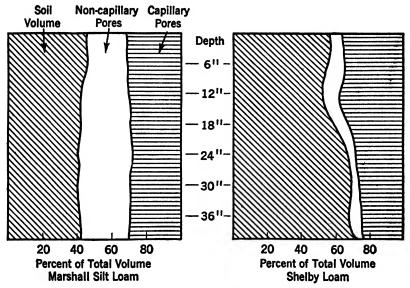
Fig. 1. Pore-space relationships in two dissimilar soils. A large proportion of noncapillary pore space is desirable because it promotes drainage and improves aeration. (*Reproduced by permission from L. D. Baver, "Soil Physics," 2d ed., John Wiley & Sons, Inc., 1948.*)

conditions also, though few data are available from field tests. Eaton and Horton (1940) reported that the wilting percentage and moisture equivalent of soils partially saturated with sodium were higher than those of the same soils treated with calcium, if most of the soluble electrolytes were first removed. It has been observed frequently that permeability of soil is reduced by irrigation of land with water containing a high proportion of sodium as compared to other bases. This is important in semiarid regions, where rainfall is too light to remove the salts concentrated in the surface layer by evaporation of irrigation water. Richards

and Fireman (1943) found that the permeability of soil saturated with sodium was much less than that of calcium-saturated soil—a condition that indicates change in structure. Even the addition of sodium in the form of sodium nitrate reduces the permeability of some soils to an undesirable extent. This occurs because sodium causes dispersion of the granules of clay into their constituent micelles, thereby reducing the pore space through which water can move.

Appreciation of the importance of soil structure has raised questions concerning the propriety of determining such soil properties as water-holding capacity, moisture equivalent, and permanent wilting percentage on disturbed soil. Soil samples are usually dried, pulverized, and passed through a 1- or 2-mm. sieve. The original macrostructure is thus thoroughly destroyed before the samples are subjected to various tests. In recent years, a number of methods have been described for obtaining soil samples without disturbing their macrostructure. Coile (1936), for example, described a method of obtaining samples that provide undisturbed soil masses for determining volume weight, water-holding capacity, and permanent wilting percentage. H. J. Lutz (1944*a*) has also made numerous determinations on samples collected in cylinders. It appears that determinations made on screened and pulverized samples usually are not seriously different from those made on undisturbed samples; but some exceptions occur, especially in the case of fine-textured soils, the properties of which are more dependent on macrostructure than those of coarse-textured soils, and in the case of certain soils of very high density (Veihmeyer and Hendrickson, 1948).

The Soil Profile. Before the discussion of soil texture and structure is dropped, it may be well for us to recall that these properties are seldom the same in the deeper layers of soil as they are in the surface layer. Most undisturbed soils possess a "profile," consisting of definite horizons or layers of soil, which differ in their properties. Thus the

upper, or A, horizon generally differs appreciably in texture and hence in field capacity and permanent wilting percentage from the B horizon, which lies below it. Sampling of the surface soil alone does not give an accurate indication of the soil characteristics or of the amount of water available to the deeper part of the root system. Furthermore, layers of sand or gravel or impervious layers sometimes occur within a few feet of the surface, and the effects of these must be taken into account in evaluating the soil moisture available to plants. When soil is sampled for determining its physical properties or its moisture content, care should be taken to make certain that each soil horizon penetrated by roots is adequately sampled.

Organic Matter. The organic matter, or humus, found in the soil represents that portion of the plant remains—chiefly the lignified material—which is most resistant to decay. Organic matter resembles clay in some respects, being colloidal, with negatively charged micelles surrounded by shells of cations, but it shows even more chemical and physical activity than does clay. Because of its very great surface, it holds a great deal of water; for this reason, an addition of organic matter to sandy soils somewhat increases their water-holding capacity. Its addition to clay may improve the texture and workability but usually has much less effect on the available water content than is commonly supposed, because the water-holding capacity of clay is already comparatively high and the unavailable water content of organic matter is very high. Feustel and Byers (1936) found that a mixture of one-half clay and one-half peat moss by volume held only about 25 per cent more available water than pure clay would, whereas a mixture of one-half quartz sand and one-half peat moss held about 800 per cent more water than pure sand would. Veihmeyer (1938) reported that addition of as much as 200 tons per acre of manure did not appreciably increase the content of water available to plants in sand, loam, or clay soils. He concluded that it is impossible to change materially the water-holding capacity

of a soil under field conditions by the addition of organic matter. Havis (1943) found that additions of 8 or 16 tons of manure per acre for 27 years did not significantly increase the available water-holding capacity of Chenango loam, but that they did increase the available water-holding capacity of Chenango fine, sandy loam.

Tukey and Brase (1938) found that young apple trees made appreciably more root growth in soil plus 50 per cent peat moss by volume than they would in soil alone, particularly if the soil and soil-peat mixtures were kept wet. This was attributed largely to improved aeration in the presence of peat.

It has been claimed that addition of a hydrophilic colloid, methyl cellulose, conserves water by reducing evaporation from the soil surface and by reducing the amount of water absorbed by plants growing in the treated soil (Felber and Gardner, 1944). Although the water requirement of plants was shown to have been reduced about one-third, it was claimed that growth was not reduced. Wadsworth (1946) was unable to demonstrate any significant reduction in water loss by adding this material to the soil and concluded that the treatment is not effective on agricultural soils. It will be seen later that as the forces with which soil moisture is held are increased plant growth is decreased. It therefore seems probable that addition of hydrophilic colloids to the soil in quantity sufficient to reduce evaporation or absorption by plants will generally result in reduction in growth.

Classification of Soil Moisture

The classification of soil moisture most familiar to plant scientists is the simple system of Briggs (1897) with the addition of water vapor, as suggested by Lebedeff (1928). This system divides soil moisture into four classes:

1. *Gravitational water,* which occupies the larger pores of the soil and drains away under the influence of gravity.

This water is often injurious to plants if drainage is too slow.

2. *Capillary water,* which is held by surface forces as films around the particles, in angles between them and in capillary pores. In the form of liquid, capillary water moves slowly from thicker to thinner films and along moisture-tension or diffusion-pressure gradients. It can also move in the form of vapor. Capillary water is the only important source of water for most cultivated plants.

3. *Hygroscopic water,* which is held as very thin films on the particles by surface forces. This water is held so firmly that it can move only in the form of vapor. The moisture remaining in air-dry soil is usually regarded as hygroscopic water and is unavailable to plants.

4. *Water vapor,* which occurs in the soil atmosphere and moves along vapor-pressure gradients. It probably is not used directly by plants.

Such a classification must be regarded as somewhat arbitrary in the light of present-day theories of soil moisture, because there really is no sharp boundary between these different classes of soil moisture. If moisture tension (defined later in this chapter) is plotted against moisture content, a smooth curve is produced without any breaks to separate these regions on the curve (see Fig. 3). Although under certain conditions capillary water may become gravitational water and hygroscopic water may become capillary water, the classification seems useful enough to be retained, in spite of its arbitrary nature; it is shown diagrammatically in Fig. 2. A brief discussion of the various types of water follows.

Gravitational Water. For a short time following a heavy rain or irrigation, the soil may be completely saturated with water, because the air has been displaced from the larger, noncapillary pore spaces between the particles. Under the influence of gravity, most of this free water soon percolates downward through the soil toward the water table, unless it is prevented by some barrier, such as a hardpan layer.

Within 2 or 3 days after a rain, all the gravitational water usually drains out of at least the upper horizon of the soil, and the noncapillary pore spaces become refilled with air. If the soil remains saturated with gravitational water for several days, serious injury to root systems may result from lack of oxygen and accumulation of excess carbon dioxide. Obviously, therefore, gravitational water is of little direct value to most plants and may be even detrimental.

Capillary Water. After the gravitational water has drained away, a soil is said to be at its field capacity. The water remaining exists as films around the soil particles, in the angles between the particles, and in the smaller, or capillary, pores. Much of this water is held rather loosely and is readily available to plants. Some capillary water, however, is held so firmly by the colloidal material and in the smallest pores that it is relatively unavailable to plants. As has been stated previously, the finer the texture of the soil, the more surface is exposed and the more capillary water it will hold. Since capillary water moves slowly, it is relatively unavailable unless the roots actually come into contact with it. In general, movement of capillary water from moist to dry soil is quite slow. The significance of this fact with respect to absorption will be discussed later.

Hygroscopic Water. The capillary water remaining in an air-dry soil is usually termed hygroscopic water. It is held in very thin films of perhaps 15 to 20 molecules in thickness. The upper limit of hygroscopic moisture is generally supposed to be the moisture content of soil in equilibrium with saturated air, but soil kept in contact with moist air over a long period of time may accumulate so much water that it will actually become saturated (Keen, 1931, page 214). This illustrates the difficulty of distinguishing sharply between these two classes of soil moisture. Hygroscopic water, if the term is used to refer to the water in the air-dry soil, is obviously unavailable to plants.

Figure 2 shows the relations between the various classes of soil moisture.
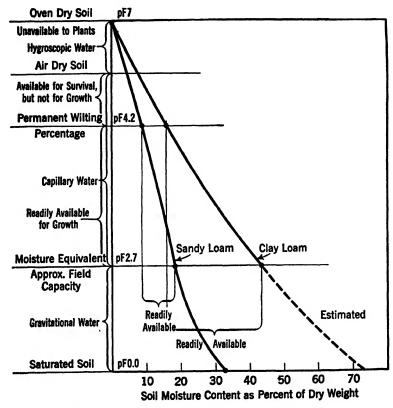
Fig. 2. Classification of soil moisture and differences in available and unavailable moisture content of a sandy and a clay soil. The clay loam contains almost three times as much readily available water as does the sandy loam.

Soil-moisture Terminology

The literature dealing with soil moisture contains numerous special terms. Many are of interest only to soil scientists or engineers, but a number of them are frequently used in discussions of plant and soil-moisture relations. Among these latter are capillary potential, moisture tension, free energy, diffusion-pressure deficit, moisture stress, pF value, capillary capacity, maximum water-holding capacity, field capacity, hygroscopic coefficient, wilting coefficient, wilting

point, permanent-wilting percentage, wilting range, moisture equivalent, xylene equivalent, readily available water, relative wetness, and water-supplying power. Some of these terms are defined in the following pages. Methods of measuring a few of the more important soil constants are described in Chap. 4.

Capillary Potential. The capillary potential, or pressure potential, of a soil is a measure of the attractive forces with which water is held by the soil. It can be expressed directly in ergs per gram or gram centimeters per gram. Since the capillary potential is difficult to measure directly, it usually is expressed in terms of the work that must be done to move water against the capillary forces of the soil. Buckingham (1907), who originally proposed this quantity, expressed it in terms of the height in centimeters of a column of water which will exert sufficient pressure to move water in the soil at a given moisture content. Technically it is a measure of work done per unit of mass in moving water from a free, flat water surface to a given point in the soil-moisture system. The potential of free water, which is the base or reference value from which the potential of soil moisture is measured, is regarded as zero. The capillary potential increases negatively with decreasing moisture content, because water is held more firmly in dry soil than in moist soil.

Moisture Tension. The moisture tension of the soil, which is the negative pressure of the soil water, includes gravitational, hydrostatic, and surface forces but not osmotic forces. Usually it is expressed in terms of the height in centimeters of a column of water or in atmospheres of pressure which must be applied to remove water at a given soil-moisture content. When expressed in terms of a water column, moisture tension is approximately equal numerically to the capillary potential in centimeters per gram. Technically it is the force per unit of area which must be applied to remove water from soil at any given moisture content. Shull (1916) made one of the earlier attempts to measure the force with which water is held by the soil. He

compared the amount of water absorbed by dry Xanthium seeds from solutions of various osmotic pressures with the amounts that they absorbed from soils of various known moisture contents. From these observations he was able to calculate the force with which water is held by the soil at various moisture contents. His curves are similar in shape to those obtained more recently by other methods. Moisture tension can be measured in moist soils by using tensiometers or by applying suction to a thin layer of soil supported on a porous porcelain membrane. Richards (1941*a*) developed a technique by which the moisture content of the soil at equilibrium with any pressure up to more than 25 atmospheres can be measured directly. Thus it is possible to plot moisture tension against moisture content; the resulting curve gives a clear picture of the availability of water to plants over the entire range of readily available moisture. While some discrepancies exist in present measurements, it appears that at the moisture equivalent the tension is equal to about ⅓ atmosphere, while the tension at permanent wilting is in the neighborhood of 15 atmospheres. Moisture-tension curves for two soils are shown in Fig. 3.

Free Energy. In recent years, use of the thermodynamic function "free energy," has been proposed to deal with soil-moisture problems (Edlefsen, 1941; Edlefsen and Anderson, 1943). This reflects the increasing tendency to emphasize that the force with which water is held by the soil is the most important soil-moisture value with respect to plant growth. We do not measure the free energy of soil moisture but rather the difference in free energy between the water in the soil and the free energy at a flat water surface, which is used as the reference point on the free-energy scale. As the water content of the soil decreases, the free energy of the water also decreases.

Two kinds of forces decrease the free energy of soil moisture. One is the osmotic force, or potential produced by solutes in the soil solution, which is expressed as the osmotic

pressure of the extracted soil solution. This increases because the soil solution becomes more concentrated as the soil dries. The other is the capillary potential—or pressure
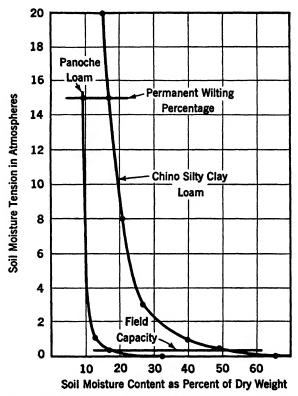
Fig. 3. The relation between soil-moisture content and moisture tension in a sandy soil and in a clay soil. The curve for Panoche loam is from Wadleigh, Gauch, and Magistad (1946). That for Chino silt clay loam is based on data from Richards and Weaver (1944).

potential—of the soil, which includes all the other forces acting on soil moisture. These are chiefly the attractive forces of soil particles, plus gravitational and hydrostatic forces. Their combined effect usually is measured as tension, in centimeters of water. The soil-moisture tension plus the osmotic potential of the soil solution equals the free energy—or, more accurately, the free-energy deficit—of soil

moisture. The free energy of soil moisture is treated as a
negative value because the application of surface forces or
the addition of solutes decreases the free energy of water.
The free energy per unit mass might be expressed in ergs per
gram, but in practice we are more concerned with differ-
ences in free energy than in absolute values. The differences
are most conveniently evaluated in terms of the pressure
required to adjust the free energy of water in another state
to that of the reference state, free water.   By applying
enough pressure to equal the tension with which water is
held by the soil particles, we can increase its free energy
sufficiently to cause it to move.

Unfortunately the free energy of soil moisture in the lower
part of the range of readily available soil moisture is diffi-
cult to measure directly, though some estimates have been
made from vapor-pressure and cryoscopic determinations.
The moisture tension at various moisture percentages can
be measured up to about 850 cm. of water by tensiometers
and suction plates and to more than 25 atmospheres by the
pressure-membrane apparatus of Richards (1941a). If the
concentration of solutes in the soil solution is negligible, the
moisture tension will approximately equal the free-energy
value, but this is not always true.   Richards and Weaver
(1944) reported, for example, that according to freezing-
point determinations the total free-energy value of certain
California soils at the moisture equivalent is over twice the
soil-moisture tension. The difference is represented by os-
motic forces, which in this instance are much too great to be
neglected.   It is therefore clear that the free-energy value
of soil moisture cannot be regarded as always equal to the
moisture tension, bcause in some soils considerable discrep-
ancies exist.

Diffusion-pressure Deficit.   Another method of express-
ing the difference in free energy between free water and
water in solution or in surface films is in terms of its dif-
fusion-pressure deficit.   The diffusion-pressure deficit of
water in a given system (in the soil or in a plant cell) is

the amount, in atmospheres, by which its diffusion pressure is less than that of pure water. The principal factors causing increase in the diffusion-pressure deficit of water are the addition of solutes; the action of surface forces, as on water held in films around soil particles; and the imposition of negative pressure or tension, as in the conducting system of rapidly transpiring plants. The concept of diffusion-pressure deficit, which has been widely used to evaluate the water relations of plant cells and tissues, is equally applicable to problems of water movement in the soil and from soil to plant. The theoretical basis of the diffusion-pressure-deficit concept has been discussed by Meyer (1938, 1945); it is applied to various problems by Crafts, Currier, and Stocking (1949) and by Meyer and Anderson (1939). The diffusion-pressure deficit of a soil is really a measure of the difference between the free energy of the soil moisture and that of free water. It is determined by the combined effects of moisture tension and osmotic forces; if the concentration of solutes in the soil solution is negligible, the diffusion-pressure deficit is approximately equal to the moisture tension.

Moisture Stress. This term was proposed by Wadleigh and Ayers (1945) to include both groups of forces that reduce the free energy of water. These groups are the gravitational, hydrostatic, and surface forces that comprise the moisture tension, and the osmotic pressure of the soil solution. Wadleigh (1946) discussed the application of the term moisture stress to soil-moisture problems, especially in soils high in salt. If it is expressed in atmospheres, the moisture stress appears to be equal to the diffusion-pressure deficit of a soil.

Soil pF. According to Schofield (1935), "The pF is the logarithm of Buckingham's potential. By analogy with Sorenson's acidity-scale the symbol p indicates its logarithmic character, while the symbol F is intended to remind us that by defining pF as the logarithm of the height in cm. of the water-column needed to give the suction in question

we are really using the logarithm of a free-energy difference measured on a gravity scale." In other words, pF is the logarithm of the capillary potential or the free energy when the latter is expressed in centimeters of water. The chief advantage of this scale is that it permits the entire range of soil-moisture tension to be shown on one compact scale, although the equivalent water column is almost 10 km. (1,000,000 cm.) at equilibrium with 50 per cent relative humidity (pF 6) and about 10 times greater at ovendryness (pF 7). The moisture equivalent is at a pF of about 2.7, the wilting percentage at about 4.2. Water may be regarded as moving along a pF gradient from regions of low pF to regions of higher pF.

Richards and Weaver (1944) pointed out that Schofield undiscriminatingly included two kinds of values in his use of pF. He proposed that it be used as a free-energy scale but included values calculated from suction plates and tensiometers, which are really moisture tensions or capillary potentials, along with true free-energy values calculated from vapor-pressure and freezing-point data. At present most people apparently use the term pF as the log of the soil-moisture tension, which is what Schofield did in practice, rather than as the log of the free energy, as he defined it. While it is true that in many soils the two values are practically equivalent, they are not always equal and the term pF ought not be used indiscriminately for both. The chief advantage of the pF scale is its compactness, an advantage that scarcely justifies its use (see Veihmeyer, 1944).

Hygroscopic Coefficient. The hygroscopic coefficient is the moisture content of the soil in equilibrium with an atmosphere of known relative humidity—usually a nearly saturated atmosphere. According to Keen (1931) and others, the experimental difficulties inherent in making such determinations render them of very doubtful value, although at relative humidities below saturation reproducible results can be obtained. This value generally is of minor interest to plant scientists.

Maximum Water-holding Capacity. The maximum water-holding capacity is the water held by a thin layer of saturated soil. The soil is placed in a shallow metal container with perforated bottom and is allowed to stand in water until it becomes saturated. This gives measures of pore space, specific gravity, and expansion on wetting. Keen (1931, page 227) commends it as a measurement useful to the soil scientist. The method of draining surplus water will affect the results obtained. The results may also vary depending on whether the measurement is made on pulverized soil or on a soil mass with undisturbed structure. Because this is not a measure of the amount of water held under field conditions it is not very useful to plant scientists.

Field Capacity. The field capacity has been referred to as the field-carrying capacity, normal field capacity, normal moisture capacity, and capillary capacity. It is the moisture content after the gravitational water has drained away and capillary water movement has become very slow (Veihmeyer and Hendrickson, 1931). It is therefore essentially equal to the capillary capacity. Most soils are at their field capacity within from a few hours to 2 or 3 days after a rain or after irrigation. Soil samples in short columns allowed to drain over sand probably reach approximately their field capacity within a few hours. Veihmeyer and Hendrickson (1936) state that this is not a true equilibrium value, but only a condition of such slow water movement that the moisture content does not change appreciably between applications of water. While most soils reach their field capacity very quickly, the presence of a water table near the surface will greatly prolong the time required for drainage. If the soil is saturated to a depth of many feet, drainage of the surface layer to field capacity will be much slower than it will if only the top few feet are wetted. Also, a fine-textured soil overlying a coarse-textured soil will have a higher field capacity than a uniformly fine-textured soil. Since field capacity is related to the soil profile and to soil struc-

ture, laboratory determinations will not always indicate what the value will be under field conditions.

Moisture Equivalent. This is a term that was introduced by Briggs and McLane (1907) to denote the water content of soil that has been subjected to a centrifugal force of 1,000 times gravity in a soil centrifuge. The precautions necessary to ensure accurate results have been discussed by Veihmeyer, Oserkowsky, and Tester (1927), among others. Veihmeyer and Hendrickson (1931) found the moisture equivalent to be closely related to the field capacity of certain fine-textured soils but not to that of sands. When Work and Lewis (1934) found that the moisture equivalent of certain Oregon soils was not equal to the field capacity, they concluded that such a relation should not be assumed without actual determinations. Browning (1941) found the ratio of field capacity to moisture equivalent to be unity when the moisture equivalent is about 21 per cent, to be more than unity for soils with moisture equivalents below 21 per cent, and less than unity for those with moisture equivalents above 21 per cent. In a very coarse-textured soil, the field capacity may be twice the moisture equivalent. Although the equipment is expensive, the determinations are so easily made that the moisture equivalent is one of the most frequently determined soil-moisture constants. Since the moisture equivalent is a purely arbitrary value— one that has been found not to be reliably correlated with permanent wilting percentage or with field capacity—it is of less usefulness to plant scientists than was formerly supposed. The soil-moisture tension at the moisture equivalent is approximately $\frac{1}{3}$ atmosphere.

Xylene Equivalent. The xylene equivalent is determined in the same manner as the moisture equivalent, except that xylene is substituted for water. According to Russel (1933), it is closely related to the amount of silt and clay in the soil. Since xylene is a nonpolar liquid, it is not adsorbed or imbibed by soil colloids, as is water. It therefore fills the micropores of the soil but, unlike water, causes no

swelling. The difference between the moisture equivalent and the xylene equivalent of a soil, which is a measure of the soil's ability to imbibe water, is termed the imbibitional water value. Russel observed that the theory underlying this determination is inadequate to establish its real meaning. Nevertheless, Coile (1948) found that the rate of growth of pine in the lower Piedmont of North Carolina depends more on the imbibitional water value of the B horizon than on any other soil characteristic.

Permanent-wilting Percentage. The moisture content of the soil at the time when the leaves of plants growing in that soil first become permanently wilted has been variously designated as the wilting point, wilting coefficient, wilting percentage, and permanent-wilting percentage. According to modern usage, it is designated as the permanent-wilting percentage. Briggs and Shantz (1912) first emphasized the importance of this soil-moisture content with respect to plant growth and termed it the "wilting coefficient." Their procedure was to grow seedlings in glass tumblers of soil sealed over with a mixture of paraffin and vaseline. When the leaves wilted and did not recover overnight in a moist chamber the moisture content of the soil was determined by ovendrying a sample at 105°C. and calculating the moisture content as a percentage of the dry weight. Briggs and Shantz stated that this marked the lower limit of soil moisture available for growth, but not the lower limit of soil moisture available to plants. Although absorption is too slow for growth at moisture contents below the wilting point, plants are able to absorb water from the soil until it is approximately air dry or until they have died of desiccation. Permanent wilting does not mark any definite limit in the movement of water from soil to plant; it simply marks the moisture content at which absorption becomes too slow to replace the water lost by transpiration, the result of which is wilting. Methods of determining this important value are given in Chap. 4.

Many species of plants will survive for considerable pe-

riods in soils drier than the permanent-wilting percentage. Taylor, Blaney, and McLaughlin (1934) found this to be true of the native vegetation of southern California. Fowells and Kirk (1945) reported that in soil in which sunflower seedlings had wilted permanently *Pinus ponderosa* seedlings survived for at least several weeks and that such seedlings recovered and grew when the soil was watered. The ability to survive periods of desiccation—an important factor in drought resistance—is possessed by many species.

Wilting Coefficient. In addition to actually determining the wilting percentage, Briggs and Shantz (1912) attempted to calculate it from the moisture equivalent. They found that, for their soils,

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84 \pm 0.013}$$

This value has been used frequently, but subsequent work by several investigators shows that such a relation does not always exist. Veihmeyer and Hendrickson (1931) investigated 60 soils and found the ratio to range from 1.4 to 3.8 (also see Table 3). Duncan (1939) found that the ratio of moisture equivalent to wilting percentage in three soils on the Duke Forest ranged from 1.57 to 5.65, varying with soil type and horizon. According to Coile and Gaiser (1947), the ratio of moisture equivalent to permanent-wilting percentage varies with the amount of clay and organic matter. Briggs and Shantz (1912) also attempted to relate the wilting coefficient to the hygroscopic coefficient, to the moisture-holding capacity, and to the mechanical analysis. More recently, attempts have been made to relate the permanent-wilting percentage to the colloid content (Wilcox and Spilsbury, 1941). The usefulness of any such cross-relating of values is obviously very doubtful, since the relations are not the same in all soils.

The Wilting Range. Taylor, Blaney and McLaughlin (1934) applied this term to the range of soil moisture from

the first permanent wilting of the basal leaves of sunflowers to the complete permanent wilting of the entire plant. Furr and Taylor (1939) and Furr and Reeve (1945) published data on this range and the latter give detailed instructions for its determination. Furr and Reeve use the terms "first permanent wilting point" and "ultimate wilting point" to designate the upper and lower limits of the wilting range. Like Briggs and Shantz, they regard the first permanent wilting point as the lower limit of soil moisture available for growth. The moisture in the wilting range, while it is unavailable for growth, is available for survival, and the proportion of the total available soil moisture within this range is great enough to be of considerable significance in plant-water relations. In about 80 soils that were studied by Furr and Reeve (1945), a minimum of 11 per cent and a maximum of 30 per cent of the moisture content between the moisture equivalent and the ultimate wilting point was in the wilting range. The wilting range is shown graphically in Fig. 4.

Readily Available Moisture. This is the moisture that can be used by plants in growth and is therefore the moisture above the permanent-wilting percentage, or first permanent wilting point. While gravitational water is readily available to plants, it usually drains off too soon to be of much importance. The readily available water, therefore, is usually considered to be that included in the range from field capacity down to the permanent-wilting percentage. In sandy soils this range is quite narrow, in clay it is quite wide. The advantages of a wide range of available water in carrying plants through droughts or in obviating the need for frequent irrigation are too obvious to need discussion. The relative availability of water in the upper and lower part of this range will be discussed later. As has been previously stated, plants can absorb water from soils drier than the permanent-wilting percentage, but under such conditions absorption is too slow for growth.

Relative Wetness. This is a term proposed by Conrad and Veihmeyer (1929) to express the ratio of moisture content to moisture equivalent. Dividing the moisture content by the moisture equivalent enables us to make comparisons of available water content between soils or soil horizons that
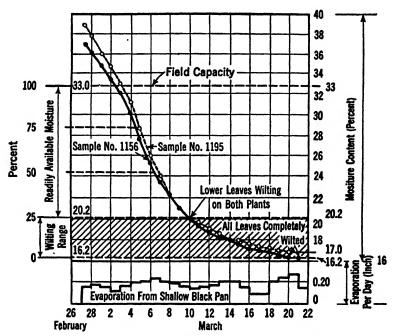
FIG. 4. Rate of removal of soil moisture by sunflower plants and the wilting range of a Meyer clay-adobe soil. (*From Furr and Taylor, 1939.*)

differ in texture. This is particularly useful in following moisture changes at various depths or in various parts of an orchard or a field where the soil is not uniform in texture. An example of this is shown in Fig. 28.

The Water-supplying Power. This refers to the rate at which water moves from soil to an absorbing surface, such as a root. This term generally is used to refer to measurements made with the "soil point cones" of Livingston and Koketsu (1920), which will be discussed later in connection with methods of determining soil moisture.

The Movement of Soil Moisture

The movement of soil moisture is relatively complex because of the various directions and states in which it moves and the various forces operating to cause its movement. Downward movement occurs when the soil is being wetted by rain or irrigation, some upward movement occurs when the surface is drying by evaporation, and a limited amount of lateral movement may occur. Water moves as liquid in capillary films and in the larger, or noncapillary, pores from regions of lower to regions of higher tension. Appreciable movement also occurs in the form of vapor along gradients from regions of higher to regions of lower vapor pressure, and in convection currents of the soil atmosphere. The forces that cause movement of liquid water are chiefly gravity, hydrostatic pressure, and capillary forces. Because frequently there is difficulty in determining precisely what forces are bringing about water movement, it is considered best to regard water as moving along gradients of decreasing free energy. This statement is true regardless of the nature of the forces involved or the terminology used to express them.

Infiltration. Infiltration of water into the surface is the first step in wetting a soil, and the rate of infiltration into a given soil is a very important factor in determining how much of a given rainfall will be accumulated in the soil and how much will be lost by runoff. The rate of infiltration decreases rapidly in most soils after only a few minutes' exposure to rainfall. This is caused by the dispersion of large soil particles by raindrops and the packing of small particles between the larger ones by surface flow, so that the pores are plugged and water cannot penetrate freely (Baver, 1948; Duley, 1939). Formation of such a layer can be avoided and runoff can be greatly decreased by crop cover, by mulches, and by the incorporation of organic matter into the surface of the soil. Bodman and Colman (1944) believe that the decrease in infiltration with time is largely caused

by a decrease in the moisture potential within the transmission zone of the soil as the wet front moves farther below the surface. Other factors are the swelling of clay when it is wetted and the entrapment of air. Deterioration in soil structure that is caused by tillage operations sometimes results in decreased permeability to water (Parker and Jenny, 1945).

In a 4-year test in the Central Valley of California, substitution of weed-killing sprays for cultivation resulted in improvement of soil porosity and water penetration and in the disappearance of plow sole (Moore, 1945). Wilson and Browning (1946) found the soil to be much better aggregated in plots in bluegrass than in plots continuously cropped with corn. Erosion was decreased and water infiltration increased on well-aggregated soil. On light, sandy soils in Florida irrigation by sprinkling is often ineffective because of difficulty in wetting the surface layer beneath the trees. Penetration of soil moisture is very uneven where such a condition has developed (Jamison, 1946). According to Duley (1939), formation of an impermeable surface layer has more effect on the infiltration of water into Nebraska soils than is due to soil type, slope, moisture content, or profile. Runoff and accompanying erosion, in his opinion, can be practically eliminated by maintaining a mulch of crop residues on the soil. While infiltration into a bare soil is much more rapid at first if it has been cultivated, the rate decreases very rapidly after the first 15 to 30 minutes, and on both cultivated and uncultivated soils it soon reaches a constant rate, which is determined by the rate of downward percolation through the deeper soil horizons. Permeability of a soil to water is markedly affected by the concentration and kind of ions present. As has been previously mentioned, irrigation with water high in sodium results in displacement of calcium by sodium; and if the salts are leached out, such soils become dispersed and impermeable. Fireman (1944) describes a soil that was 20 times as permeable to tapwater and 35,000 times as permeable to water con-

taining 800 p.p.m. of calcium chloride as it was to distilled water.

Movement of Water through the Soil. The earlier discussions of the movement of soil moisture were based on a relatively simple concept of the soil as an aggregate of capillary tubes of various dimensions, and many present-day discussions make use of this capillary theory. According to this theory as developed by Briggs (1897), soil moisture exists principally as continuous thin films around the soil particles and in the smaller spaces and angles between them. These films are under great inward pressure because of the surface tension of the water; water, therefore, tends to move from regions with thicker films to regions with thinner films.

While the foregoing assumptions are correct, the capillary theory has been found inadequate to explain certain observed facts. It has, therefore, been sharply criticized. Dissatisfaction with the inadequacy of this theory led to the gradual development of another, based on the energy relations or work done during the movement of water. Buckingham (1907) suggested that movement of water through the soil might be compared to the movement of heat or of electricity through a conductor. He considered the driving force to be the difference in attraction for water between two portions of soil having different moisture contents, and he proposed the term "capillary potential" for the force required to move a unit mass of water from a unit mass of soil. This theory was further developed by Gardner (1920), Keen (1931), Richards (1928), and by others. For more detailed discussions of various aspects of this theory, the reader may refer to these writers and to Baver (1948), Russel (1942), and Edlefsen and Anderson (1943).

The most important implication of the potential theory of soil moisture is that there are no such sharp boundaries or differences between various types of soil moisture as are indicated by the terms gravitational, capillary, and hygroscopic water. Various methods of measuring the potential or force with which water is held by soil at various moisture

contents agree in indicating that the potential is directly related to the moisture content. When the potential is plotted against decreasing soil moisture, it forms a smooth curve (see Fig. 3), indicating that there is no real change in state of water as it decreases from the field capacity past the wilting percentage down to the hygroscopic coefficient, but merely an increase in the energy required to move it. The permanent-wilting percentage falls beyond the region of greatest curvature of the curve for tension over soil moisture, while the field capacity falls in the region where it becomes almost flat.

Edlefsen (1941) and Edlefsen and Anderson (1943) propose that the thermodynamic concepts of free energy be applied to discussions of water movement in the soil and through the plant. Such a treatment of soil-moisture movement is based on sound principles and is very useful to the soil physicist. Unfortunately, however, most plant scientists are not sufficiently familiar with the mathematical methods used to understand such a treatment. To many workers it is more intelligible and for most purposes it is just as satisfactory to discuss the movement of moisture in the more familiar terms of diffusion pressure, vapor pressure, or diffusion-pressure deficit—all of which are also based on energy relations. The plant scientist is primarily concerned with understanding the factors that affect the availability of water and its movement from soil to plant roots. The movement of soil moisture can be discussed in conventional terms if we remember that, regardless of the terminology, this movement is determined by differences in energy or in the forces with which it is held in different regions of the soil. Using this conventional terminology, we may say that water flows under the influence of gravity, moves in capillary films, and diffuses as vapor, but that it always moves along a gradient from regions of higher to regions of lower free energy.

Movement of Gravitational Water. The movement of gravitational water is affected chiefly by number, size, and

continuity of the air spaces, or noncapillary pores, through which it percolates. As it usually moves very freely through the large pores of sandy soils, such soils as a rule are quickly drained to field capacity. Movement is less rapid through clay, because the pores are much smaller, they are frequently blocked by the swelling of colloidal gels, and air is often trapped in them. Lutz (1934) found the permeability of clay to decrease as the hydration of the particles increased. Movement of gravitational water is frequently hindered by impermeable subsoil layers, which trap air as well as water. Movement is facilitated by the penetration of worms and the activity of other animals, and by the decay of roots—all of which leave passageways. In general, unless a hardpan interferes or the soil is saturated to a shallow water table, gravitational water can be expected to drain out of the surface layer from within a few hours to 2 or 3 days after rain or irrigation, the time required depending on soil texture and subsoil conditions. Figure 5 shows the rate of downward movement beneath an irrigation furrow.

Movement of Capillary Water. Since so-called capillary water is the principal source of moisture for plants, its movement is of particular interest. When water is applied to a dry soil by rainfall or by irrigation, it moves downward partly under the influence of gravity and partly by capillarity. A very limited amount of horizontal movement also occurs by capillarity. The force that causes capillary movement is largely the difference in surface tension between films that have different thicknesses and angles of curvature, as movement proceeds from thicker to thinner films. If these forces are expressed in terms of "tension," water moves along a gradient from a region where the forces holding water are low to one where they are higher—in other terms, from a region of low pF to one of high pF, from a region of high vapor pressure to one of lower vapor pressure, or from one of low diffusion-pressure deficit to one of high diffusion-pressure deficit.

Regardless of the terminology, water always moves along
a gradient of decreasing free energy. Its free energy is

Distance from Center of Furrow, Inches

| 30 | 24 | 18 | 12 | 6 | 0 | 6 | 12 | 18 | 24 | 30 |

Ground Surface

0

12

Depth from Bottom of Furrow, Inches

24

36

48

60

Slight movement
of moisture below
72 in. with 48
hr. run

Moisture passed
below 72 in. with
72 hr. run

72

MOISTURE MOVEMENT

| 1 Hour | 4 Hours | 8 Hours | 24 Hours | 48 Hours | 72 Hours |
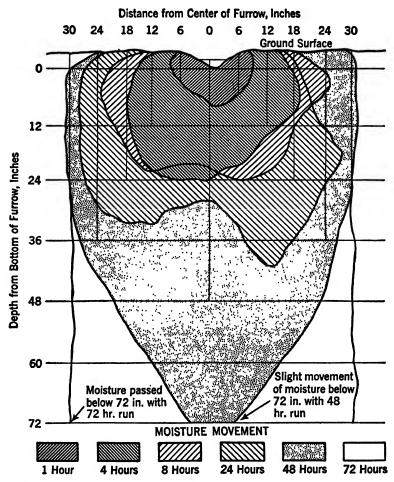
Fɪɢ. 5.   Infiltration of water into Yolo loam from an irrigation furrow kept
filled for various lengths of time. Note that vertical movement exceeds
lateral movement. (*From Hendrickson and Veihmeyer, 1933.*)

highest in free water, lower in moist soil, and still lower in
dry soil. Movement of capillary water is materially affected
by soil texture, being most rapid in sandy soils and slowest
in clay soils at saturation; but in drier soils the effects of

texture are reversed, movement being slowest in sands and most rapid in clay (Moore, 1939). Height of capillary rise also depends on texture, being greatest in clays and least in sands. In no instance, however, has capillary rise been found to be as great as would be expected from calculations based on size of soil particles; nor has the movement of capillary water proved to be as rapid as it was once supposed to be. Early discussions of this subject gave the impression that as rapidly as water is removed from the soil particles in contact with the roots it is replaced by capillary movement from more distant soil particles. More recent investigations indicate that capillary movement of soil moisture from moist to drier regions is very slow, except where the water table is within 3 or 4 ft. of the surface. Of course, some movement always occurs from regions with thicker films to regions with thinner films, provided that continuity of films exists; but such movement is much more rapid in saturated soil than in dry soil. Moore (1939) found very little unsaturated flow of moisture in soil at or below the moisture equivalent. Veihmeyer and Hendrickson (1927) placed in a large cylinder a mass of soil that was wet to field capacity, with dry soil on each side of it. After 139 days, water had moved only 8 in. into the dry soil.

It has been found that the curve for wetting and that for drying of a soil, as indicated by tensiometers, are somewhat different. Richards (1941b) found that the moisture content of a soil could be decreased to bring it into equilibrium with a tension of 0.5 atmosphere in 1 to 3 days; but if the start was made from air-dry soil, a much longer time was required to attain equilibrium by wetting. A period of 180 days was required for all the soil in a 6-in. autoirrigator pot to be wetted from the air-dry condition to a condition of equilibrium with a tension of only 150 cm. of water. These facts further illustrate the differences in rate of water movement in wetting and in drying soil, as well as the relatively slow rewetting of a dry soil by capillarity.

Since capillary movement is quite slow in soils drier than

field capacity, it is probable that during periods of rapid transpiration the available water on soil particles in contact with the roots is removed much faster than it can be replaced by capillary movement. Thus each absorbing root may become surrounded by a slender cylinder of soil from which practically all available water has been removed, although soil a few millimeters away is still at field capacity. Data of Richards (1941a), however, indicate that water movement may occur over short distances more rapidly than is commonly supposed. He found that a pressure of 16 atmospheres reduced the moisture content of a soil layer 5 to 10 mm. in thickness, from saturation to below the permanent-wilting percentage, in 24 to 36 hours. Richards and Weaver (1944), after further investigation with the pressure-membrane apparatus, reported that measurable water movement occurs in soils in the wilting range. Movement apparently occurs as flow in the surface films, because it is more rapid than can be accounted for by diffusion of vapor. These investigators regard such movement as important in prolonging the survival of plants during drought conditions, although it could scarcely contribute enough water to permit growth. While movement of measurable amounts of water occurs over a distance of a few millimeters in soil in the wilting range, movement of liquid water over greater distances probably is negligible.

Movement of Water Vapor. As the soil dries out, the water films become discontinuous and capillary movement ceases. Any water movement in air-dry soils must be in the form of vapor. According to Lebedeff (1928), the atmosphere in soil above its hygroscopic coefficient is normally saturated. Under field conditions, therefore, the soil atmosphere is always saturated, except in the surface layer, which occasionally becomes air dry. Movement of water vapor is along vapor-pressure gradients; hence it is affected by the relative temperatures and vapor pressures of various horizons of the soil and of the soil and air. Lebedeff found the movement of water in the form of vapor to be of con-

siderable importance, especially in southern Russia and other semiarid regions where there is no direct connection between the water table and the capillary water in the upper layer. Since film movement is exceedingly slow under such conditions, the effects of movement of water vapor are more noticeable. Lebedeff found that in the winter appreciable quantities of water move from warmer, deeper levels to the cooler surface, where it condenses, the amount so moving in one winter amounting to 66 mm. During a cool period in summer or autumn, when the surface layer is cooled, water moves from the deeper levels to the surface, from whence it evaporates during warmer periods, thus slowly drying out the deeper layers. Ordinarily the surface layer of the soil is warmest during the summer. Presumably at that time some water vapor diffuses downward and then condenses in the cooler soil, forming liquid water. According to Lebedeff, this is an important source of ground water in southern Russia. During the night, the surface layer becomes cooler than the soil a few centimeters below the surface, while the reverse is ordinarily true during the day. These diurnal variations in soil temperature produce variations in vapor pressure, which result in diurnal variations in water movement. Lebedeff calculated that in the vicinity of Odessa over 70 mm. of water are condensed in the surface layer of soil annually, during periods when it is cooler than the air above it. In California, Edlefsen and Bodman (1941) observed considerable upward movement of water vapor in soil during the winter and downward movement during the summer.

Smith (1944) claims that moisture movement along a thermal gradient can occur by a combination of vapor movement and capillarity, an initial transfer in the form of vapor producing an unstable condition, which is followed by capillary movement. Any reader who desires a more detailed discussion of soil-moisture movement is referred to Baver (1948).

CHAPTER 3

FACTORS AFFECTING THE SUPPLY OF SOIL MOISTURE

The amount of soil moisture available for plant growth, except in areas where irrigation is practiced, depends on the amount of precipitation. This usually is measured in inches per year, but the total amount of rainfall per year is not a reliable indication of its effectiveness in supporting plant growth.

Effectiveness of Precipitation

The effectiveness of a given amount of precipitation in promoting plant growth depends on how much of it reaches the soil mass occupied by roots and can be stored there. This depends on numerous factors, including the seasonal distribution of rainfall, topography, soil texture, amount of evaporation, and the type of plant cover.

If a large percentage of the precipitation occurs in the winter and relatively little in the summer, as takes place along the western coast of the United States, less vegetation will be supported than in regions where heavy precipitation occurs during the growing season. Even though the average precipitation during the growing season appears adequate, the distribution may be so erratic that summer droughts often limit plant growth, as is true of the Prairie and Plains regions. Summer precipitation occurring in frequent light showers is less effective than precipitation that occurs in rains of 0.5 in. or more, because of the larger percentage lost by evaporation from light showers. On the other hand, "downpours" are ineffective because during such rains a large percentage of water is lost by runoff, instead of

soaking into the ground. The effectiveness of precipitation also varies according to the amount of evaporation, which depends on the humidity of the air, temperature, and amount of wind. As a result of the high temperature and low humidity, the percentage of rainfall dissipated by evaporation is much greater in the southern part of the United States than that in the northern part. Although 15 to 20 in. of precipitation is enough for many crops in North Dakota, it produces only enough vegetation for grazing in Texas, where evaporation is much higher.

Evaporation and Transpiration Compared to Precipitation

Numerous measurements of the amounts of water lost by evaporation and transpiration have been made in various localities. Over the United States as a whole, about one half of the total precipitation runs off in stream flow and about one half is returned to the atmosphere by evaporation and transpiration, but wide local variations occur (Meinzer, 1942, page 321; Lyon and Buckman, 1943).

In a Sierra Nevada forest where the annual rainfall was 43 in., Kittredge (1937) calculated that runoff amounted to 26 in., or 60 per cent of the total. Of the remaining 17 in., approximately 6 in. was intercepted by the vegetation, 3 in. evaporated from the soil surface, and about 8 in. was lost by transpiration. On the other hand, in areas of limited rainfall, such as the Great Plains, water loss may exceed total precipitation. Wiggans (1936, 1937, 1938) observed that in 18- to 20-year-old apple orchards in eastern Nebraska evaporation and transpiration removed 10 to 15 in. more water per year than was replaced by precipitation. In one year, for example, the equivalent of 37.8 acre-in. of water was removed, but only 22.6 in. was returned, with a resulting deficit of 15.2 acre-in., which came from the reserve of available moisture in the deeper layers of soil. Wiggans stated that growth was already reduced in some of these orchards and estimated that in 3 more years all available water would be exhausted to a depth of 30 ft.

Unless irrigation is provided, orchards will soon die when this condition is attained.

Many forest trees in the plantations established in the Prairie and Plains regions under the Timber Claim Act, in the 1880's and 1890's, grew well for a number of years but eventually became unthrifty and began to die, especially those trees in the center of the plantation. This probably was caused by exhaustion of available moisture in the whole soil mass occupied by their roots. Bunger and Thomson (1938) reported that rainfall in the panhandle of Oklahoma is inadequate for indefinite growth of trees, although they can grow for some years on reserve soil moisture. In such regions, trees mature at an early age and die when the reserve soil moisture is exhausted.

A similar situation exists with respect to certain perennial herbaceous plants on deep soils in areas of limited rainfall. In Nebraska, Kiesselbach, Russel, and Anderson (1929) found that although newly seeded alfalfa makes excellent growth for about 3 years, quite independent of current rainfall, the yield thereafter declines and becomes closely correlated with current rainfall. The decline evidently is caused by depletion of available moisture in the subsoil during the first 3 years, after which yield is dependent on the amount of rainfall. Alfalfa may absorb soil moisture to a depth of 30 ft. in well-aerated soils, and this is replaced very slowly. After 15 years of cropping to cereals, following alfalfa, very little moisture had been replaced below the 7-ft. level. It was estimated that, at the present rate, 225 years would be required for replacing the soil moisture removed in only 6 years by a stand of alfalfa.

Even in areas of much higher average precipitation, water usage sometimes exceeds rainfall during the growing season. Reimann, Van Doren, and Stauffer (1946) studied the water relations of a corn crop on a silt loam soil near Urbana, Illinois, during a rather dry summer. About 10.2 in. of rain fell from June 1 to Sept. 15. Of this, 2.0 in. were intercepted by the corn plants and lost by evaporation, while

8.2 in. soaked into the soil. About 5.3 in. of water were lost from the soil surface and 8.2 in. were removed by the transpiring corn plants. Thus the total water loss exceeded by 5.3 in. that entering the soil, and the difference was supplied from water stored in the soil, the amount of available water in the upper 7.5 ft. of soil being reduced from 12.4 to 7.1 acre-in.

Water Loss by Evaporation

The quantity of water lost from soil by evaporation has been the subject of considerable controversy. The amount of water vapor lost depends primarily on the steepness of the vapor-pressure gradient from soil to air. This in turn depends on both soil and atmospheric factors. The vapor pressure of the atmosphere is affected chiefly by the temperature and the humidity of the air. Air movement also is important, because it prevents the air in contact with the soil surface from becoming saturated. The principal soil factors affecting evaporation are the temperature and the moisture content. Differences in evaporation from dark- and light-colored soils and from north- and south-facing slopes result from differences in temperature.

It is obvious that evaporation from a soil will be much decreased when the surface becomes dry, because diffusion of water vapor through the soil is very slow. When no rainfall occurs, the principal way in which the soil surface can be kept moist is by upward capillary movement of water; hence it has long been assumed that prevention of capillary movement by cultivation will greatly reduce loss by evaporation. Experiments by King (1914) showed that, from soil covered with a loose, dry surface layer 2 or 3 in. deep, less than half as much water was lost as from an undisturbed surface. King's experiments were with columns of soil in contact with free water. According to Baver (1948), Eser had already shown in 1884 that evaporation from soil in contact with free water is two to four times as fast as evaporation from well-drained soils. Unfortunately most people

have failed to realize that evaporation from soil that is in contact with a water table occurs much more rapidly than evaporation from soil that does not have a water table near the surface. As a result of this misunderstanding, the advantages of a dust mulch in agricultural practice have been greatly overemphasized.

More recent experimental work has shown that evaporational losses are less than has been commonly supposed and that they are not much reduced by cultivation. This is primarily because the water table is so far below the surface in most cultivated land that little upward movement to the surface can occur. Considerable experimental evidence is available indicating that if the water table is even a few feet below the surface little upward movement of water occurs. Shaw and Smith (1927) found considerable water movement to the surface of Yolo sandy loam and Yolo loam with a water table 4 ft. below the surface, but very little when it was 10 ft. below the surface. They concluded that no appreciable upward movement of water to replace loss by evaporation occurs in these soils when the water table is 10 ft. or more below the surface. Keen (1928) found very limited rise of water in large cylinders of soil 6 ft. high. Veihmeyer (1938) cites experimental evidence concerning the slow movement of capillary water in soils. Table 2 shows the effect of depth of water table on rate of evaporation. Where rainfall seldom or never wets the soil to the water table, as in much of the plains area, upward movement is probably negligible. In most soils, more water is removed by transpiring plants than by evaporation.

Work in Russia and in this country indicates that little water is lost by evaporation from below the first foot. Veihmeyer (1927) stated that under California conditions most of the water lost by evaporation comes from the upper 4 in., much less from the second 4 in., and very little from below 8 in. By the time that the surface soil has dried sufficiently to permit cultivation, considerable moisture has already been lost, and more is lost from the freshly stirred

Table 2. Average Evaporation from Water-logged Soils at Davis, California *

Depth to water table, feet	1936, inch per day	May 15– Sept. 1, 1937, inch per day	Mar. 29– Nov. 10, 1937, inch per day
0.0	0.328	0.317	0.216
0.5	0.215	0.230	0.182
1.0	0.209	0.194	0.162
1.5	0.093	0.086	0.076
2.0	0.079	0.055	0.051
3.0	.....	.....	0.026
4.8	. ...	. ...	0.016

* From Veihmeyer (1938).

soil, hence cultivation sometimes increases evaporational losses. In general, most soil appears to dry out to about the same extent and the same depth, whether it is cultivated or not, unless the water table is within a few feet of the surface. Cultivation might reduce loss by evaporation on soils that crack badly, but Veihmeyer and Hendrickson (1936) claim that the cracks in most California soils, including clays, are too shallow to increase water loss seriously. Cultivation of summer-fallowed land may, of course, be necessary to prevent a crop of weeds from removing all the accumulated moisture. More extensive discussion of this problem can be found in Lyon and Buckman (1943), Chap. X.

Loss of water by evaporation from the surface layer of soil probably is serious only when much of the precipitation occurs in light rains. This is particularly important where summer rainfall is stored by summer fallowing. Burr (1914) reported that in western Nebraska a rainfall of 0.5 in. or less is entirely dissipated by evaporation unless the surface soil is still moist from a previous rain. He found that 10 to 33 per cent of the season's rainfall could be stored by summer fallowing, the amount being less if rainfall oc-

curred in showers than if it was concentrated in soaking rains. Burr seems to have been one of the earliest investigators to show that capillary movement of water in the soil is very slow and that capillary rise to the surface is of negligible importance unless the water table is within a few feet of the surface.

While dust mulches seem to be ineffective, it appears that mulches of straw, grass, leaves, paper, and similar materials are usually much more effective in reducing water loss. This is partly because they shade the soil, reducing its temperature, and partly because they lengthen the diffusion gradient from soil to air and protect the soil surface from the drying effects of wind. Russell (1939) considers mulches to be effective only in preventing drying of the surface layer, because a layer of dry soil is a better insulator than is the average mulch and also because it is more impervious to water vapor.

Evaporation versus Transpiration

A considerable amount of water is intercepted by the plant cover and never reaches the soil surface, because it evaporates directly into the air. The amount lost in this manner is greatest from forests and least from grasslands, and the proportion thus dissipated is much greater when rainfall occurs as light showers than when it occurs as heavy rains. During a rather dry summer, about 20 per cent of the rain falling on an Illinois cornfield was intercepted by the corn plants and lost by evaporation before it reached the soil (Reimann, Van Doren, and Stauffer, 1946). According to Kittredge (1937), interception by a Douglas fir forest may exceed 40 per cent of the summer precipitation, and over large areas interception by forests may amount to 10 to 25 per cent of precipitation. Haynes (1940) states that a considerable fraction of the water intercepted by leaves of crop plants eventually reaches the soil by running down the stem.

The relative amounts of water removed from the soil by

evaporation and by transpiration are of interest, particularly in regions of limited rainfall. It is generally agreed that transpirational losses exceed losses by evaporation where well-developed grasslands and forests occur. If evaporation removes water only from the surface foot of soil, the remainder of the soil moisture would remain untouched were it not for the roots of plants. Orchard soils in the East are sometimes dried to the wilting percentage to a depth of 2 or 3 ft. within 3 weeks (Magness, Degman, and Furr, 1935) and prune trees exhaust the readily available water in the top 6 ft. of soil in about 6 weeks in midsummer at Davis, California (Hendrickson and Veihmeyer, 1934) (see Fig. 6). Veihmeyer and Hendrickson (1936) state that mature peach trees in the Sacramento and San Joaquin valleys of California absorb the readily available water from sandy soil to a depth of 6 ft. in about 3 weeks. Citrus fruits on sandy loam soils 4 to 6 ft. deep, in San Diego County, require irrigation every 6 weeks during the summer. On more shallow soils irrigation is required more frequently. In such instances loss by transpiration must be several times greater than loss by evaporation.

Veihmeyer (1938) describes experiments in which a tank with bare soil surface lost 18.9 lb. per sq. ft. of surface over a period of 4 years, equivalent to a depth of $3\frac{3}{8}$ in. of water. A 4-year-old prune tree growing in a similar tank lost 1,250 lb. of water by transpiration in one growing season. An acre of deciduous fruit trees at Davis, California, used 8 acre-in. of water in about 6 weeks in midsummer, or about 1 lb. per sq. ft. of soil surface per day. Pillsbury, Compton, and Picker (1944) state that in the interior zone of San Bernardino and Riverside counties, California, transpiration of vigorous citrus trees averaged 21 acre-in. and that of trees in fair condition, 17 acre-in. in a season. Transpiration thus accounted for from 50 to 80 per cent of the total water applied during the irrigation season. R. J. Weaver (1941) found that about 85 per cent of the water loss from a stand of *Andropogon furcatus* in a Nebraska prairie was

by transpiration and about 15 per cent by evaporation from the soil surface. Where the Andropogon was pastured, losses by evaporation and transpiration were about equal. Total water loss from the pasture was about 55 per cent of the loss from the unpastured prairie with its greater transpiring surface.
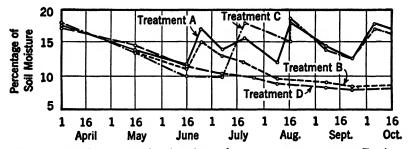

FIG. 6. Rate of removal of soil moisture by mature prune trees at Davis, California. The soil is Yolo loam with a moisture equivalent of 20 per cent in the top 3 ft., and 14.5 per cent in the 3- to 6-ft. level. The permanent-wilting percentages are 10 and 9 per cent in the upper and lower levels. The average moisture content of the upper 6 ft. is shown on the graph. Treatment *A* was irrigated four times, as shown by the four peaks in moisture content. Treatment *B* was irrigated once; treatment *C*, three times, beginning July 11. Treatment *D* was not irrigated, hence it remained near the permanent-wilting percentage most of the summer. (*From Hendrickson and Veihmeyer, 1933.*)

Hydrologists are concerned with the amount of water lost by transpiration and evaporation, because it affects the water reserves of an area. Transpiration may even be great enough to cause daily fluctuations in the height of the ground-water table. In the Escalante Desert of Utah it was found by White (see Meinzer, 1942, page 438) that the water level in test wells began to fall at 9 to 11 A.M. and reached its lowest level at 6 to 7 P.M., then rose during the night. The maximum fall in level was about 1.5 in. with greasewood and shadscale, 2.5 in. with alfalfa, and 4.5 in. with sedges and marsh grasses. Numerous measurements have been made by hydrologists of what they term consumptive use of water. This is the total amount of water

lost by evaporation plus that absorbed or intercepted by the plant cover of an area. These sources of loss are combined because it is difficult or impossible to measure them separately over a large area. Measurements of consumptive use have been made by growing crop plants and native vegetation in large containers. It is necessary to surround such containers with a belt of the type of vegetation being tested or the amount of water used will be far in excess of that used under natural conditions. Taylor (1934) found the loss from a tank of tules set in the open to be 3.5 times as great as that from a tank set in the marsh along the tules.

Large-scale measurements have been made by determining the difference between the inflow and the outflow of entire valleys over a period of years. Results of such measurements are summarized by Lee in Meinzer (1942). He concluded that in California hydrophytes are the heaviest users of water. Tules and cattails use 5 to 8 ft. of water per year, and alder, cottonwood, and sycamore all use more than 4 ft. per year. Plants using 3 to 4 ft. per year include most of the grasses and, where the summers are warm and the water table is high, alfalfa. Most field crops, orchards, and vineyards use 1.5 to 2.5 ft., except in the delta of the Sacramento and San Joaquin rivers, where the consumption is 2.0 to 3.0 ft. In cooler regions, where the growing season is shorter, less water is used. Native grasses and shrubs on well-drained soil in arid or semiarid regions also remove less water than do crop plants, doubtless partly because they produce less transpiring surface per acre. It has been observed that the water consumption is much greater if the water table is near the surface than if it is at a depth of several feet. In general it appears that, on an acre basis, considerably more water is lost by transpiration if the supply is always abundant than if it is somewhat limited at times. This is partly because larger shoots are produced when there is an abundance of water and partly because the rate of transpiration in this case is less often retarded by wilting and stomatal closure.

In general, considerably more water is lost from an area by transpiration than would be lost by evaporation from the same soil surface if it bore no vegetation. It therefore appears that maintenance of vegetation on a watershed decreases the amount of water that can be obtained from it. Kittredge (1936) suggested that since plant cover is essential to control erosion and to slow down runoff, species with low transpiration rates should be selected. He recommended scrub oaks and grasses for California watersheds. Forest cover intercepts a considerable amount of rainfall, which never reaches the ground, hence grass might be a more satisfactory ground cover in locations where water yield is very important. Wilm (1946) has summarized recent views on this subject.

Additional papers dealing with these problems can be found in the *Transactions of the American Geophysical Union,* Section of Hydrology, the *Journal of Forestry,* and state and Federal bulletins. Much valuable information has been summarized in a book entitled "Hydrology" edited by Meinzer (1942) and in a recent book by Kittredge (1948).

The Availability of Soil Moisture to Plants

The availability of soil moisture depends primarily on the tension or force with which it is held by the soil. This is, of course, related to the moisture content, the tension increasing as the moisture content decreases. It depends also on the concentration of the soil solution and, to a limited extent, on the kinds of ions present in the soil. Low soil temperatures also decrease the availability of soil moisture.

Soil-moisture Content. The gravitational water occurring in saturated soils, although it is readily available to plants, is seldom present long enough to contribute much to plant growth. If it does remain more than a day or two, the injurious effects of it usually overshadow any benefits resulting from its availability. For most plants, then, the water readily available for growth is the so-called capillary

water in the range between the field capacity and the permanent-wilting percentage. The best moisture supply for growing plants is afforded by soils in which this range of available water is wide. Soils show great variations in this respect, but sandy soils generally have narrow ranges of available water and clay soils have wide ranges (see Fig. 2 and Table 3). Occasionally, however, soils that have high field capacities also have very high wilting points and contain but little available water. An example of this type is the Aiken clay loam of Table 3. This table, abridged from one compiled by MacGillivray and Doneen (1942) shows soils having a wide range of variation in capacity to hold readily available water.

Table 3. Storage Capacity of Various Soils for Readily Available Water *

Soil type	Moisture equivalent	Permanent-wilting, percentage	Ratio M.E./P.W.P.	Inches of available water per foot, depth
Oakley fine sand.......	3.29	1.33	2.47	0.34
Yolo fine sandy loam...	16.80	8.93	1.88	1.26
Aiken clay loam.......	31.12	25.70	1.21	0.71
Salinas silt clay loam...	28.33	12.49	2.26	2.53
Salinas clay...........	34.50	16.80	2.05	2.83
Catherine loam........	37.90	19.03	1.99	3.08
Wooster silt loam......	23.36	6.12	3.82	2.89
Brockton clay loam....	24.51	11.55	2.12	1.98
Plainfield fine sand.....	2.40	1.36	1.76	0.17

* From MacGillivray and Doneen, 1942.

Plants growing in soils that have so low a storage capacity as the Oakley fine sand or the Aiken clay loam of Table 3 will exhaust the readily available water and suffer from drought much sooner than will plants growing in such soils as the Catherine loam or the Wooster silt loam, which have a large storage capacity. Where irrigation is practiced, the more frequent applications required on a soil having limited

storage capacity result in much greater waste of water by runoff and evaporation than will occur on soils with a large storage capacity, where fewer irrigations suffice.   This is especially important in the case of shallow-rooted crops. Veihmeyer and Hendrickson (1938a) cite several examples of such occurrences.   The coarse, sandy loam used by Kramer and Coile (1940) holds about 1.2 in. of available water per foot of depth, whereas their clay soil holds about 2.2 in.   Plants growing on the sandy loam obviously will suffer from drought sooner than will those on the clay.   The Chino silty clay loam soil shown in Fig. 3 contains about three times as much available water as does the Panoche soil.

Depth of soil also is important, because a deep soil holds more water than a shallow one underlain by impermeable strata.   Drought injury is much more frequent and severe on shallow soils.   Magness, Degman, and Furr (1935) concluded that in the Middle Atlantic states it is unwise to grow apple trees on soils less than 3 or 4 ft. deep.   If the soil holds less than 10 to 12 per cent of available water, it should be more than 4 ft. deep to assure a fairly dependable supply of moisture.

Some discussion has occurred as to whether water is equally available over the entire range from field capacity to wilting percentage.   Veihmeyer and Hendrickson have repeatedly stated that water either is available or is not available to plants, and that it is equally available over the entire range from field capacity down to the wilting point, where it becomes unavailable for growth.   They have reported results of experiments indicating that the growth and quality of apples, grapes, peaches, pears, prunes, walnuts, and cotton are not affected by the moisture content of the soil unless it falls to the wilting percentage and remains there for some days.   These plants did no better on frequently irrigated plots than on plots where the soil moisture was allowed to fall to the wilting percentage before water was applied.   According to Maximov (1929), Kokina

reported that the growth of various herbaceous species was found to be largely independent of water content until the soil moisture reached a very low level. Magness, Degman, and Furr (1935) reported that the growth rate of apples was not reduced by decreasing soil moisture until at least the driest part of the root zone reached the wilting percentage. Doneen and MacGillivray (1943) found that the seeds of many species germinate equally well over the entire range of moisture content, from wilting percentage to field capacity. A few, however, germinated better at 1 or 2 per cent above field capacity, and celery seed did not germinate at all in the lower range of soil moisture.

Results of other experiments cast doubt on the view that water is equally available over this entire range. Aldrich and Work (1934) and Lewis, Work, and Aldrich (1935) reported that in very heavy soils in Oregon the rate of growth of pears is closely related to the moisture content of the upper 3 ft. of soil. The fruits suffered reduction in size when the soil moisture dropped below about 70 per cent of the readily available moisture. Trees in these soils have very uneven root distribution, and it may be that, while the soil in contact with the roots was at the permanent-wilting percentage, considerable volumes of soil not penetrated by roots were left at field capacity. As a result, the average moisture content would appear to be above the wilting percentage, although the moisture content of the soil surrounding the individual roots was actually reduced to the wilting percentage. Schopmeyer (1939) found that the transpiration rate of loblolly and shortleaf pine seedlings grown in containers decreased with decreasing moisture content while the soil was still above its permanent-wilting percentage. This, likewise, might have resulted from uneven absorption of water because of uneven distribution of root systems.

Furr and Taylor (1939) reported that lemons growing in shallow soil underlain by dense subsoil suffered sufficient water deficit to cause reduction in the size of the fruit before

the moisture content of all the soil in the top foot was reduced to the permanent-wilting percentage. They suggested that some discrepancies in conclusions regarding the availability of water result from differences in judgment as to what constitutes permanent wilting. In a heavy clay soil having a field capacity of 33 per cent, the basal pair of leaves of well-established sunflower plants wilted at 20.2 per cent, but the entire plants did not wilt until the soil moisture was lowered to 16.2 per cent (see Fig. 4). Recently Furr and Reeve (1945) reported that a decrease in soil moisture from field capacity to the permanent-wilting percentage (first permanent wilting of basal leaves) caused the osmotic pressure of plants in dry air to increase about 5 atmospheres and that of plants in moist air to increase 2.5 atmospheres. They concluded that plants are subjected to progressively increasing water deficit from a moisture content about halfway between the moisture equivalent and the permanent-wilting percentage down to the permanent-wilting percentage.

Davis (1940) reported that growth of young maize plants was slowed by decreasing soil moisture and that it ceased before the soil-moisture content fell to the wilting percentage. Water appeared to be less available for growth from a moisture content 2 or 3 per cent below capillary capacity, and growth ceased while 3 per cent of available water remained in the soil. Haynes (1948) also reported that, in fertile, well-aerated soil, growth of corn plants increased with increasing soil moisture almost to saturation. Davis (1942) found that when *Cyperus rotundus* was grown in pots, growth appeared to be checked by decreasing availability of water in soil which was always above the wilting percentage. Each decrease in the minimum soil-moisture percentage that was reached before rewetting to saturation resulted in a significant decrease in weight of the tops of Cyperus. Tuber development was decreased significantly by decreasing soil moisture only 2 per cent below the moisture equivalent.

Daubenmire and Charter (1942), in contrast, reported that growth of seedlings of several species of desert legumes continued unchecked until the moisture content of the soil reached the permanent-wilting percentage, then ceased abruptly. Long (1943) reported that adding 100 milli-equivalents of sodium chloride per liter, which results in a solution with an osmotic pressure of about 4 atmospheres, caused severe wilting of tomato plants. He suggested that, if water is equally available to plants from the field capacity to permanent-wilting percentage, a range of about 15 atmospheres, increasing the osmotic pressure of the water surrounding their roots by 4 atmospheres, should not have seriously interfered with absorption. Hayward and Long (1943) also found that high solute concentration increased moisture stress and seriously checked growth of tomatoes. Ayers, Wadleigh, and Magistad (1943) and Wadleigh and Ayers (1945) found the growth and yield of kidney beans to be reduced if the soil was allowed to dry partway down to the permanent-wilting percentage before watering, even though the moisture content never actually reached the permanent-wilting percentage. According to Scofield (1945a), larger yields of alfalfa are produced when the plants are continuously supplied with water by subirrigation than when they are watered intermittently, although never allowed to wilt.

From the standpoint of energy involved in movement of water from soil to plant, there can be little doubt that soil moisture becomes less and less readily available as the moisture content decreases from field capacity to the permanent-wilting percentage. As the moisture content of the soil decreases, there is inevitably an increase in the amount of energy required to move a unit mass of water a unit distance. In another sense, however, at least in light soils, soil moisture may be practically as readily available to the plant at moisture contents just above the wilting percentage as at the field capacity; that is, in the sense that under some conditions water may be absorbed and transpired at the same

rate in drier soils as in soils at the field capacity. This is because, as the moisture content of the soil and the moisture content of the plant decrease, the osmotic pressure and the diffusion-pressure deficit within the plant increase. While an increase of a few atmospheres in the diffusion-pressure deficit of the roots may supply the increased energy gradient necessary to maintain a high level of absorption, it does not appreciably reduce transpiration. In a sandy soil thoroughly permeated with roots, plants might reduce almost the entire soil mass nearly to the wilting percentage before transpiration decreases or the plants exhibit symptoms of a deficit. In heavy soils where root distribution is variable and sparse, as in the lemon orchards of southern California and the pear orchards at Medford, Oregon, the water is not uniformly absorbed from the entire soil mass and one cannot say that there is a definite moisture content above which water is available and below which it is unavailable.

There is little doubt that water is not equally available to detopped root systems over the range from field capacity to permanent-wilting percentage. It has been observed frequently that removal of the tops from unwilted herbaceous plants is not always followed by the expected exudation of sap from the stumps, even after several hours have been allowed for the satisfaction of an internal water deficit. It has been found (Kramer, 1941) that exudation from the stumps of coleus, sunflower, and tomato growing in sandy loam ceased while about 45 per cent of the soil moisture available to intact plants was still present. Similar results were obtained with sunflower in coarse sand and in clay. This situation probably results from the fact that the roots alone cannot absorb water with a force of more than 1 or 2 atmospheres, but when attached to a transpiring shoot they can develop much greater forces and therefore are able to absorb water from much drier soil. This view agrees with the observation of Furr and Reeve (1945) that plants are subjected to progressively increasing water deficit with

moisture contents less than halfway between the moisture equivalent and the permanent-wilting percentage.

For practical purposes, however, in many sandy soils water may be regarded as being equally available over most of the range from field capacity to permanent wilting. This is because the moisture-tension curve of most soils is hyperbolic (Fig. 3) and most of the range of readily available water lies in the flat portion of the curve. Most of the readily available water is removed from light soils before the tension on the remainder exceeds 1 atmosphere, and only a small fraction is held with sufficient force to hinder absorption. This is not true, however, in heavy clay, where 50 per cent or more of the available water sometimes is held with tensions in excess of 1 atmosphere. In such soils water actually does become limiting to growth before the moisture content is reduced to the permanent-wilting percentage. These differences are illustrated by the curves for Panoche loam and Chino silty clay loam in Fig. 3.

Concentration and Composition of the Soil Solution. The concentration and the composition of the soil solution have important effects on plant growth beyond their role as a source of nutrients, particularly in the more arid parts of the world. Considerable areas support little or no plant growth because of excessive concentrations of salts in the soil. Alkali soils, known in the southwestern United States as "black alkali," contain an excessive concentration of exchangeable sodium. This affects the physical properties of the soil by producing a high degree of dispersion of the soil colloids. As a result, such soils have low permeability to water and gases, poor drainage, and poor aeration, all of which are unfavorable to plant growth. Alkali soils usually have, besides, high pH values, rendering such elements as iron and manganese unavailable, but their most distinctive characteristics are related to their physical structure. Saline soils, sometimes known as "white alkali" soils, are characterized by the presence of a high concentration of salts, but these soils do not usually become so badly dis-

persed as do the "black alkali" soils. The principal factor hindering plant growth in saline soils is the reduced availability of water resulting from the high diffusion-pressure deficit of the soil solution.

For many years it has been known that the concentration of salts in the soil solution in some areas is too high for successful growth of crop plants. A survey of conditions in the Southwest indicated that normally productive, irrigated soils have a soil-solution concentration at the permanent-wilting percentage of 1.3 to 1.8 atmospheres. Some soils having osmotic pressures at the permanent-wilting percentage of 2 to 4 atmospheres produce satisfactory crops of alfalfa, cotton, sugar beets, and even wheat; but usually soil solutions having osmotic pressures of 4 atmospheres or higher seriously reduce yields, even of salt-tolerant species (Magistad and Reitemeier, 1943). These field observations are supported by laboratory experiments which have shown serious reduction in the yield of alfalfa, kidney beans, cotton, flax, peaches, tomato, and various grasses when these were grown with salt concentrations producing osmotic pressures of 3.5 to 4.0 atmospheres. There is some evidence that, at least to some species, certain ions are more toxic than others. Experiments at the U.S. Regional Salinity Laboratory at Riverside, California, indicated, for example, that growth of beans and peaches is reduced more by chlorides than by sulfates; but growth of flax, guayule, and some grasses is affected more by sulfates. Magnesium salts appear to be more toxic to beans than are calcium or sodium salts. Ionic effects are believed by some investigators to be less important than are the osmotic effects of high salt concentration in reducing the availability of water to plants (see Fig. 35), but they cannot be disregarded completely.

Effects of an excess of certain ions on soil structure are also of much importance, as has been previously mentioned. Irrigation with water that is high in sodium greatly decreases permeability of the soil to water and causes other

detrimental physical changes. These effects can be mini-
mized by means of good drainage and the application of
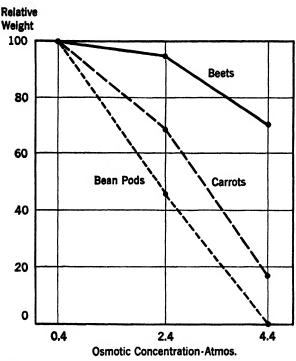calcium, preferably in the form of gypsum.

FIG. 7. Differences in effect on plant growth of differences in concentration
and osmotic pressure of the nutrient solution. (*From Magistad, Ayers,
Wadleigh and Gauch, 1943.*)

Unfortunately, the concentration of the soil solution
tends to increase in most irrigated soils. The water used
in the West for irrigation contains from 0.5 to 5.0 tons of
salts per acre-ft. Thus, depending on the quantity and
quality of water used, 1 to 10 or more tons of salt may
be added per acre in a single season; and most of it
remains when the water is absorbed or evaporated. This
accumulation can be prevented by adding enough water to
leach out the salts, but this is often impossible because of

lack of water or of adequate drainage to remove the surplus water and salt. Salt accumulation has, therefore, become a serious problem in all the major irrigation districts of the West. The practical aspects of this problem have been summarized by Hayward and Magistad (1946), while Magistad (1945) has reviewed the extensive literature in this field.

Salt concentration seldom becomes high enough to hinder plant growth in the cultivated soils of the eastern United States because frequent rains ordinarily leach the salts out of the surface soil. It is said that during summer droughts in the corn belt nutrients sometimes become concentrated in the upper 3 or 4 in. of soil as a result of evaporation of water. This temporarily depletes the supply in the absorbing zone. Salts also tend to concentrate in the outer layer of soil and in the adjacent walls of porous pots, because of evaporation of water from the surface of the pots. The concentration of roots toward the outside of the soil mass in pots is said to be caused by the higher concentration of nutrients in that region, rather than by better aeration, as is commonly supposed (Jones and Haskins, 1935).

In greenhouse soils, in which large quantities of fertilizer are commonly used, salts reach toxic concentrations more frequently than is generally realized. Merkle and Dunkle (1944) found that about 20 per cent of the Pennsylvania greenhouse soils examined by them contained excessive concentrations of salts. Davidson (1945) claimed that most of the poor growth observed in greenhouse soils that had been sterilized and used again was caused by excessive concentrations of salts.

Seed germination of many species is affected even more than is the subsequent growth of the plants. Dunkle and Merkle (1943) reported that soybeans are very sensitive, germination being reduced by the equivalent of 150 lb. of fertilizer per acre applied in rows. Their results suggest that it is inadvisable to apply too much fertilizer to seed-

beds, lest germination be reduced. This inference is supported by the observation of Uhvits (1946) that the higher the osmotic pressure of the substrate, the lower the percentage and the slower the rate of germination of alfalfa seed. Germination was practically inhibited at an osmotic pressure of 12 to 15 atmospheres of sodium chloride. Mortality of seedlings was very high in sand cultures containing sodium chloride solutions having an osmotic pressure of 7 to 9 atmospheres. Sodium chloride was found to be much more toxic than mannitol solutions of equal osmotic pressure. The poor germination was attributed to interference with water absorption, because the moisture content of seeds in the more concentrated solutions was very low.

Appreciation of the importance of the concentration of the soil solution has resulted in various attempts to measure it. Magistad and Reitemeier (1943) extracted the solution from a number of soils by the pressure-membrane method of Richards and determined both the osmotic pressure and the conductivity of the extract. In evaluating the availability of water for plants, it would be more satisfactory to measure cryoscopically the osmotic pressure of the soil solution, because the total moisture potential (free energy) of a soil equals the sum of the osmotic pressure and the moisture tension, both of which are usually expressed in atmospheres. This is time consuming and requires special equipment, hence a simpler method is needed for routine measurements in the field and the greenhouse. Some attempts have been made to measure the conductivity of soil wetted to the consistency of a paste, but such measurements are not regarded as reliable. Reitemeier and Wilcox (1946) found measurements on saturated soil unsatisfactory and recommended that conductivity measurements be made on soil solution extracted under pressure. Wilcox (1947) suggested that for routine work the soil might be wetted to a multiple of field capacity, stirred, and let stand overnight, measurements being made on the liquid above

the settled soil.   Merkle and Dunkle add 50 ml. of distilled water to 25 gm. of air-dry soil, shake for 30 minutes, and filter; then measure the conductivity of the filtrate.   They tentatively set the maximum value for satisfactory germination of most seeds at a conductivity of 200×10^{-5} mho for extracts obtained in this manner.

Soil Temperature.   Temperature of the soil measurably affects the availability of water to roots of plants.   Richards and Weaver (1944) found the water retained at 0.5 atmosphere and 15 atmospheres pressure was appreciably greater in amount in cold than in warm soil.   While temperature affects the surface forces and vapor pressure, its most important effect is probably exerted through the change in viscosity of the water itself.   The viscosity of water is only half as great at 25°C. as at zero, and Kramer (1934) found that the water-supplying power of the soil, as measured with Livingston soil-point cones, is nearly twice as great at 25°C. as at zero.   Thus the physical effects of low soil temperature have to be taken into account, along with its physiological effects on the roots, in order that the effects of low soil temperature on absorption of water may be evaluated.   Effects of soil temperature on absorption will be discussed in more detail in Chap. 9.

CHAPTER 4

MEASUREMENT AND CONTROL OF
SOIL MOISTURE

Since the moisture content of the soil so frequently is an important factor in plant growth, various methods have been devised to measure changes in it. Such terms as "wet," "moist," and "dry" soil are relatively meaningless and should be avoided if possible. Even when they are expressed on a percentage basis, measurements of soil moisture are of little value to the plant scientist unless their relation to the permanent-wilting percentage and the field capacity or the moisture equivalent is made known. A moisture content on a percentage basis which would indicate saturation of a sandy soil might be below the permanent-wilting percentage of a heavy clay soil. It is necessary, therefore, to determine the moisture content of a given soil at field capacity and at the permanent-wilting percentage before the percentage-moisture content can be evaluated in terms of its effect on plant growth.

Gravimetric Methods

The basic and most used method of determining the moisture content of soil is to collect samples in tightly closed cans, weigh them, remove the covers, dry to constant weight in an oven at 105 or 110°C., and reweigh them. The loss of weight represents the water content. If this is divided by the dry weight of the soil, the result is the moisture content on a dry-weight basis. All other methods are more or less indirect, because the measurements obtained by them are always correlated with percentage-moisture content as determined by oven-drying.

In some respects, it would be better to express the moisture content on a volume basis, because our primary interest is the volume of water available to the roots occupying a given volume of soil. It would also be easier to convert soil-moisture content expressed on a volume basis into inches of water per foot of soil or into acre-inches—terms commonly used by hydrologists in irrigation practice. If water is supplied by the acre-inch, it is necessary to know how many inches of water will be required to wet the root zone in a field or an orchard. In spite of its theoretical advantages, few measurements of soil moisture are made on a volume basis, because it is difficult to obtain soil samples of known volume. While it can be done with soil samplers, such as those described by Coile (1936) and by Lutz (1944a), this is much more laborious than obtaining samples with a spade or a soil auger. Furthermore, the presence of rocks, roots, and animal burrows in the samples frequently causes considerable variation in actual volume per sample, necessitating the collection of numerous samples to obtain reliable average values. Despite the difficulties, the information obtained from determinations made on a volume basis is so useful in calculating the volume of water available to plants in a given volume of soil that it will often justify the extra work required for obtaining it. If the volume-weight or apparent specific gravity of a soil is known, the moisture content on a volume basis can be calculated from the content on a weight basis by multiplying the percentage on a weight basis by the apparent specific gravity of the soil. Obviously, if a soil contains 20 per cent of water by volume, it contains 0.2 ft. or 2.4 in. of water per foot of depth.

Attempts have been made to shorten the time required for oven-drying by substituting chemical methods. Bouyoucos (1931) found that if a weighed sample of soil is thoroughly dispersed in a given volume of pure methyl alcohol all of the water will dissolve in the alcohol, producing a change in its specific gravity. This can be meas-

ured accurately by a hydrometer and the moisture content can be calculated, the entire process requiring less than 15 minutes. It also is possible to remove the water by allowing it to react with calcium carbide, forming acetylene gas, which escapes from the container (Sibirsky, 1935). Neither method is sufficiently reliable, however, for accurate soil-moisture determinations. Oven-drying, tedious as it is, seems to be the only reliable primary method of determining the moisture content of a soil sample. The methods to be described later are secondary in the sense that they are calibrated in terms of the gravimetric method.

The ovendrying method has several disadvantages, particularly if numerous determinations are to be made. Collection of samples requires much manual labor, weighing is time consuming, expensive ovens are required for drying, and a delay of at least 24 hours occurs before the moisture content is known. Furthermore, removal of samples disturbs root systems and only a limited number of samples can be obtained from a given area of soil. It is, therefore, impossible to follow changes in moisture content in a restricted area from day to day. Several methods have been devised for measuring moisture content of soil in place, without disturbing it. These include electrical measurements of resistance, capacitance, and thermal conductivity, and the use of tensiometers, soil-point cones, gravimetric absorption blocks, and devices to measure mechanical resistance of the soil.

Soil-point Cones and Gravimetric Blocks

Apparently, the first successful measurements of soil moisture in place were made by Livingston and his coworkers. Livingston stated that the capacity of the soil to supply water to roots is the essential factor in plant-soil water relations and that all other factors, such as texture and water-holding capacity, are important only as they affect the water-supplying capacity of the soil. He developed porous porcelain cones, called soil-point cones, to

measure the water-supplying power or capacity quantitatively (Livingston and Koketsu, 1920; Wilson and Livingston, 1932). Soil-point cones are hollow, conical pieces of unglazed porcelain, waterproofed except for an absorbing zone (see Fig. 8). They are oven-dried, weighed, placed in
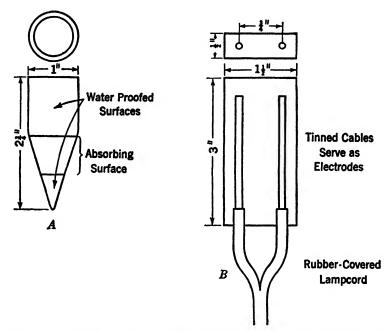

FIG. 8. *A*. Diagram of a Livingston soil-point cone. *B*. Diagram of a plaster-of-paris resistance block.

contact with the soil for a definite period of time—usually 1 hour—then reweighed and dried for further use. The increase in weight indicates how much water moves from the soil to an absorptive surface of a given area in a given time, termed by Livingston the water-supplying power of a soil. The water-supplying power of a soil is closely related to its water content, particularly in dry soils, and it is approximately the same in all types of soil at the wilting point. Soil-point cones have therefore been used successfully to indicate when irrigation is needed. The

chief difficulty with them is that they are unreliable in wet soils, and it is difficult to place them in good contact with dry, hard clay, or with gravelly soils.

Recently an attempt was made by Davis and Slater (1942) to use this principle in such a manner as to permit successive determinations in the same spot. A small, porous gypsum chamber is installed in the soil and a closely fitting gypsum plug is placed in this chamber in such a manner that it can be lifted out for weighing and then replaced. Theoretically this device should be quite sensitive at moisture tensions below 1 atmosphere and should show changes up to 4 atmospheres tension, but according to Kelley, *et al.* (1946) they have considerable lag and are not very satisfactory. Slater and Bryant (1946), however, claim to have improved them so that they are quite accurate. Richards and Weaver (1943) have described a modification of the gravimetric-block method in which the block is suspended in a tube driven into the soil and is weighed in place by means of a portable balance. It may be that by the use of proper material a gravimetric block will be developed that will be capable of field use, to indicate the need for irrigation.

Electrical Resistance

Near the end of the last century, attempts were made to measure changes in soil moisture by means of changes in electrical conductivity or resistance. These early attempts were unsuccessful, because other factors such as variations in electrode contact, temperature, and salt content of the soil produced changes in resistance which obscured the changes produced by variations in soil moisture. The most serious of these difficulties were eliminated by Bouyoucos and Mick (1940) when they imbedded the electrodes in small blocks of plaster of paris. The electrodes are thus held firmly in place in a mass of material of uniform porosity the resistance of which changes directly with its moisture content (see Fig. 8). These blocks are buried in the soil and,

after equilibrium has been established between block and soil, the block will gain or lose moisture as the soil gains or loses. This will cause easily measurable changes in resistance. It is much easier to measure resistance than conductance, hence the resistance of the blocks is measured in ohms. If the conductance is desired, it can be calculated easily, since it is the reciprocal of the resistance. The blocks can be buried at any depth in the soil and left in place for several months, leads being run to the surface for connection to a portable conductivity bridge. Resistance blocks can be purchased ready for use (see Bouyoucos and Mick), or they can be cast according to instructions given by Anderson and Edlefsen (1942).

For precise work, the blocks must be carefully calibrated. Anderson and Edlefsen recommend that they be calibrated in containers of soil thoroughly permeated by plant roots in order that a steep moisture gradient from block to soil will be produced and equilibrium between moisture content of the block and the surrounding soil will be rapidly attained. Kelley (1944) described a speedier method of calibration, for which the blocks are enclosed in a thin layer of soil in a wire basket lined with cloth. After the soil mass has been wetted and allowed to drain, it is exposed to dry air for 5 hours, then placed in a humid chamber for 19 hours, to prevent further evaporation while equilibrium is attained between the block and the surrounding soil. The weight and the conductivity are recorded and the process is repeated until the soil is air dry. Thus a record of a series of resistances and equivalent moisture contents is obtained, from which a calibration curve can be constructed.

For most purposes it is probably unnecessary to calibrate the blocks in each soil, because the resistance of all comparable blocks at a given point on the moisture-tension curve, such as the field capacity or the permanent-wilting percentage, is about the same in all soils. According to Bouyoucos and Mick (1947), comparable blocks which have a resistance of 440 to 450 ohms when saturated with dis-

tilled water at 20°C. have a resistance of 600 ohms at field capacity and about 75,000 ohms at the permanent-wilting percentage. Since all the readily available water occurs in this range, it is possible to plot a curve showing the percentage of readily available water present in any soil at
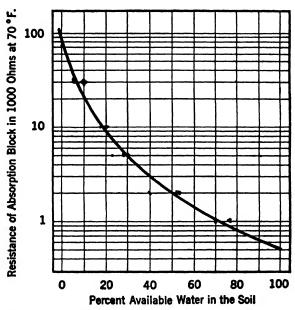

FIG. 9. Relation between amount of available soil moisture and the resistance of a plaster-of-paris block. (*From Bouyoucos and Mick, 1947.*)

any observed resistance. Such a curve is shown in Fig. 9. Bouyoucos and Mick (1947) also describe an improved bridge for measuring the resistance of the blocks. The plaster of paris tends to disintegrate if it is left in the soil for long periods of time, disintegration being most rapid in wet soils, especially those high in organic matter. The life of a block in soil of this nature is said to be about 1 year, while in relatively dry soils such a block may last 5 years.

Plaster-of-paris resistance blocks—sometimes known as Bouyoucos blocks—have been tested under a variety of

conditions and found to give a fairly reliable measure of changes in soil moisture, from field capacity down to permanent wilting. Although not very sensitive in wet soils, they become increasingly sensitive to changes in soil moisture as the soil dries out and, hence, are particularly effective in soils drier than field capacity. They are being used to some extent in irrigation practice, to indicate when water should be applied (Dahlberg and Maxson, 1942). If reliable results are to be obtained, it is essential that the blocks be so located in the soil that they will become surrounded by roots. Otherwise, they will not indicate changes in moisture content that are due to absorption. Appreciable errors are caused by wide variation in soil temperature; if the temperature is recorded, correction can be made for this. Some error is caused by variations in concentration of salts in the soil solution, but this is said to be minimized by the buffering effect of the dissolved calcium sulphate in the gypsum block. The salt error, which is probably important in soils of arid regions, is apparently negligible in humid regions. Colman (1946) described a unit to measure resistance, consisting of two electrodes mounted on a plastic disk and separated by several layers of Fiberglas fabric. The resistance of the Fiberglas between the electrodes changes with change in moisture content of the surrounding soil. This type of unit has less lag than plaster-of-paris blocks and also is said to be more sensitive in moist soil. An improved form of this unit now on the market incorporates a Thermistor in the soil-moisture element, permitting accurate measurement of soil temperature. By means of a portable meter unit, both the resistance of the soil and its temperature can be determined.

Electrical Capacitance

Since water has a high dielectric value (insulating value), and most other substances have a relatively low value, changes in moisture content of most substances are accompanied by measurable changes in dielectric value. The

dielectric value is the ratio of capacitance of a condenser system in a given medium to its capacitance in air. This method has been used to measure moisture content of seeds, flour, and dehydrated foods. Fletcher (1939) described an instrument for measuring changes in dielectric value of the soil, using electrodes which could be left in place for a series of measurements. Anderson and Edlefsen (1942) found that the electrical capacitance of a plaster-of-paris block containing electrodes such as those used for conductivity measurements varies according to its moisture content. Change in capacitance can therefore be used as a measure of change in soil-moisture content. Since capacitance is unaffected by temperature or by salt content, it would have definite advantages over electrical conductivity, if reliable measurements could be made. Anderson (1943) believes that capacitance can be measured by inserting a probe type of electrode into the soil; because capacitance, unlike conductivity, is not affected by varying contact between soil and electrode. Wallihan (1946) also regards this method as promising. It deserves further investigation.

Thermal Conductivity

Since the conduction of heat by soil decreases as the moisture content decreases, it has been proposed that thermal conductivity be used as an index to moisture content (Shaw and Baver, 1939). Enameled copper wire is wound around pieces of glass tubing and buried in the soil; then a carefully controlled current is passed through the wire for 1 or 2 minutes, causing a rise of temperature, which can be measured by the change in conductivity of the wire. The magnitude of the temperature rise depends on the rate at which heat is conducted away; this is related to the moisture of the soil. In an attempt to reduce the variability in results produced by poor contact between the heating unit and the soil, Johnston (1942) enclosed the units in plaster-of-paris blocks. Haise and Kelley (1946) found that the thermal-conductivity blocks were less satis-

factory than the electrical-resistance blocks, because at soil-moisture tensions greater than 4 atmospheres the change in moisture content is too small to affect the thermal conductivity measurably, but it does produce measurable changes in electrical conductivity. This situation might possibly be remedied by using some material other than plaster of paris for the blocks. Since thermal conductivity is not affected by salt content and since the apparatus will simultaneously measure soil temperature and soil moisture, it deserves further attention to see if it can be improved.

Tensiometers

In recent years, tensiometers have been widely used to measure the "tension" or capillary potential of the soil moisture. They consist essentially of porous porcelain cups, which are filled with water and buried in the soil and are connected by tubing to mercury manometers or vacuum gauges for indicating the pressure, or tension, on the system when the water in the cup is in equilibrium with the water in the soil. A detailed description of the construction and installation of the standard type of tensiometer is given by Richards (1942) (see also Fig. 10). Hunter and Kelley (1946c) described a model with a hinged top, which can be laid flat on the ground to allow a cultivator to pass over it. Other improvements are described by Colman, Hanawalt, and Burck (1946). Stoeckler and Aamodt (1940) described several types of tensiometers which they found useful in controlling irrigation of forest nurseries on sandy soils. If a tensiometer is installed below the surface of the water table, it will show positive pressure. In saturated soil under no hydrostatic pressure it will show zero pressure, and in unsaturated soil it will show negative pressure or tension.

According to Richards and Weaver (1944), tensiometer readings at field capacity vary considerably with the soil but are in the neighborhood of $\frac{1}{10}$ atmosphere. The tension at the moisture equivalent is about $\frac{1}{3}$ atmosphere, and at

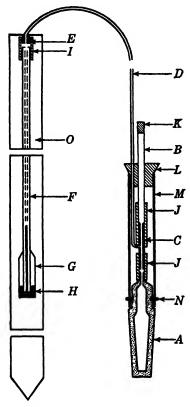the permanent-wilting percentage it is about 15 atmospheres.   The lower tension values may have been affected

FIG. 10. Construction of a soil tensiometer. Many other forms of tensiometers have been constructed. *A*, porous clay cup placed in contact with the soil; *B*, 0.5-in. glass tube, 5 in. long; *C*, 0.5-in. copper tube, 2 in. long, with 3-ft. piece of ⅜-in. copper tubing (*D*) soldered into it; *E*, a ¼-in. pipe plug soldered to end of *D*; *F*, a glass capillary tube, 1.5-mm. bore and 18 in. long; *G*, glass vial 0.5 by 2 in.; *H*, mercury; *I*, vacuum-tubing connection; *J*, vacuum-tubing connection; *K* and *L*, rubber stoppers; *M*, 1-in. brass tube, 6 in. long; *N*, setscrew; *O*, wooden support for scale. (*From Post and Seeley, 1943*.)

by the fact that they were determined on air-dried, screened soil samples and that in the 1-atmosphere range the moisture content and moisture tension are closely related to

soil structure. A tensiometer will indicate the tension on the water in the soil fairly accurately to about 0.85 atmosphere, or a little over 850 cm. of water; but as the tension approaches 1 atmosphere, air begins to leak into the system through the porous cup, rendering it inactive. Tensiometers, therefore, become inoperative when from 10 to 50 per cent of the readily available water is still present, the remaining amount being least in sandy soils and greatest in clay. Nevertheless, they are quite useful in following changes in soil moisture within their range and as a guide to irrigation where it is desired to keep the soil quite moist. A tensiometer apparently does not give the same curve in a soil that is being dried as in one that is being wetted, but this probably is unimportant under field conditions.

Scofield (1945b) tested various methods of calibration and decided that the best method is to place the tensiometer in a container filled with soil from the area chosen for the field studies and then to grow plants over it. After the plants are well grown, they are allowed to dry out the soil, the decrease in moisture content being followed by frequent weighing of the container, and the change in moisture tension by the tensiometer readings. If this process is repeated several times, a number of values are obtained, from which a calibration curve can be constructed. Scofield describes the preparation of conversion tables to show for each unit of tension the total water content or the available water content, on a volume or weight basis. Tensiometers ready for use can now be purchased.

Mechanical Methods

Methods have been devised to measure the plasticity or stability of a soil in terms of the force required to cause penetration of a plunger into a soil core. The higher the moisture content, the less is the resistance offered; therefore, calibrating the pressure against the moisture content makes it possible to determine quickly the approximate moisture content of a soil. The method is most suitable for medium

to heavy soils and cannot be used in light soils that are too dry to form soil cores. Presence of gravel also would interfere with the success of this method. An apparatus was developed by Allyn and Work (1941) for use by orchardists and others who wish to determine when to irrigate but do not have time or equipment for making more precise measurements. Shaw, Haise, and Farnsworth (1943), concluding that there is no simple relationship between soil moisture and penetrometer readings, still regard them as useful in diagnosing soil conditions.

Choice of Method

The method which should be chosen for measuring soil moisture depends somewhat on what use is to be made of the information. It is generally agreed that from the standpoint of plant growth the primary consideration is not the percentage of water present in a soil, but the availability of the water. This is dependent upon the concentration of solutes in the soil solution and upon the attractive forces of the soil particles expressed as moisture tension. The soil solution can be extracted and its osmotic pressure measured cryoscopically, to determine the importance of osmotic forces. In most soils of humid regions the moisture tension is by far the most important factor affecting the availability of water to plants and, hence, is the factor which presumably should be measured in such areas. The moisture tension at various soil-moisture percentages can be measured directly to nearly 1 atmosphere by tensiometers and over a range of decreasing soil moisture that extends well below the permanent-wilting percentage (15 atmospheres) by the pressure-membrane apparatus of Richards (1941*a*). It can be measured indirectly at high tensions by electrical methods, such as resistance blocks, or by sorption blocks, because these can be calibrated against tension measurements made at various moisture percentages. If a series of measurements on a given area is desired, tensiometers will yield good results in moist soils and electrical·

resistance blocks will be satisfactory for following the general trend of soil moisture. Slater and Bryant (1946) claim that gravimetric blocks are better than resistance blocks in at least part of the moisture range. It appears that the most valuable information concerning the availability of water in a given soil is a curve for tension at various percentage-moisture contents, from field capacity to permanent wilting—that is, over the range of readily available moisture. This does not take into account the osmotic pressure of the soil solution, a factor of great importance in semiarid and irrigated soils.

No matter how much emphasis is placed on the energy concept of soil moisture, the interest of plant scientists centers on the range of readily available water. This necessitates determination of two arbitrary values, the field capacity and the permanent-wilting percentage. At one time it was believed that both of these could be calculated from the moisture equivalent, but unfortunately this is not true; hence, both should be measured independently in every soil under consideration.

Determination of Field Capacity

The field capacity of a soil is usually described as the moisture content of a soil after most of the gravitational water has drained away and movement of soil moisture has become so slow that it can be regarded as negligible. Work and Lewis (1934) considered it to be the moisture content of a heavy soil 3 or 4 days after irrigation. In the cases of intermediate to coarse-textured, well-drained soils, it may be regarded as the moisture content a day or two after a rain or after irrigation. Since field capacity is related to the character of the soil profile, laboratory determinations cannot be regarded as exactly equivalent to those obtained in the field. As a rule, however, columns of soil which are saturated and then allowed to drain while the lower ends are in contact with soil or fine sand will have a moisture content approximating their field capacity.

Colman (1947) and Lutz (1944a) recommend that the soil be wetted and allowed to drain *in situ* before sampling for determining field capacity. Colman found that when soil was wetted to a depth of 4 ft. soil moisture in the upper 2 ft. was at field capacity after 24 hours. It was recommended by Colman (1944) that the soil be wetted to a considerable depth below the point where samples are to be obtained, because shallow wetting results in lower moisture contents than does deeper wetting. Colman (1947) reported that, if small blocks of soil are drained on a porous ceramic plate under a tension of ⅓ atmosphere, the moisture content will approximately equal the field capacity of most soils, though considerable deviations occur in very coarse- and very fine-textured soils.

Determination of Permanent-wilting Percentage

The soil chosen for determining the permanent-wilting percentage usually is air-dried and screened through a 2-mm. sieve. The exact quantity is immaterial, some workers using pint cans and 400 to 500 gm. of soil while others use larger containers and twice as much soil. For certain purposes, buckets or tubs large enough to contain small trees have been used successfully. Cardboard ice-cream containers, preferably given an extra coat of paraffin, also can be used.

The general procedure is to place weighed amounts of soil in containers, add enough water to wet the soil to field capacity, and plant sunflower seed. If the soil is infertile, enough fertilizer should be added to ensure vigorous growth. It is difficult to start seedlings in soil that is very heavy. Some workers have found it desirable to start the seedlings in greenhouse soil and then to transplant them into the soil that is to be tested (Work and Lewis, 1934). Furr and Reeve (1945) found that dipping the root systems in a soil suspension before transplanting hastened recovery. If the cans used are provided with covers, before the covers are placed on the cans, holes are punched in them for the seed-

lings to project through. The seedlings should be kept well watered and, preferably, should be grown in full sun until three or four pairs of leaves are developed. At this stage, the soil is wetted to field capacity and the hole in the lid is plugged with cotton. If no cover is used, the soil surface may be covered with a paraffin seal, as originally suggested by Briggs and Shantz. The plants are left unwatered until the lowest pair of leaves wilt. The plants are then placed in a humid chamber overnight and, if the wilted leaves recover, are next set out in a shaded place until the leaves again wilt. When the lower leaves remain wilted overnight in a humid chamber, it may be assumed that the soil in the container is at the permanent-wilting percentage. One or two samples of soil are now taken from the region of maximum root distribution in the container, all large pieces of root discarded, and the moisture content determined by oven-drying. Some workers take two samples, one from the upper and one from the lower part of the container, while others dry the entire container of soil, making a correction for the moisture content of the roots.

Furr and Reeve (1945) distinguished very precisely between the first permanent wilting point and the ultimate wilting point. As a second check on the time of first permanent wilting, they recommended daily measurements of stem elongation, because stem elongation usually ceases at the same time that the first pair of leaves wilt permanently. The ultimate wilting point is the soil-moisture percentage at which all leaves are permanently wilted. To determine this, after the first pair of leaves wilt, the plants are left in a shaded place until the apical leaves are badly wilted. At this stage, the lower leaves usually are dead, but the terminal leaves and bud will still recover if the soil is watered.

The Forest Soils Laboratory of the Duke University School of Forestry makes many permanent-wilting percentage determinations of undisturbed soil masses, in order to obviate disturbance of the natural structure of the soil. Samples are collected with a soil sampler of such size that

they fit into pint cardboard ice-cream containers. If the soil is too heavy to start seedlings directly, they are sometimes started in a layer of greenhouse soil placed on top of the sample. Oat seedlings have been used extensively in this work because their roots penetrate the soil mass very uniformly.

Various workers have developed techniques which differ in detail, but there are certain conditions which are essential to successful measurements. The plants must be grown under such conditions that their root systems are distributed throughout the soil mass. To accomplish this, the entire soil mass must have been wetted to field capacity, but it must never be saturated with water. The soil should not be packed too tightly in the container, lest there be too little pore space for good aeration. The plants must have vigorous tops bearing healthy leaves, and they should not be allowed to wilt so severely that the lower leaves will be killed before the plants are placed in a humid chamber. Determinations should be replicated, to increase the reliability of the results.

Factors Affecting the Accuracy of Permanent-wilting-percentage Determinations. The moisture content of the soil at the time of permanent wilting might conceivably be affected by the species and condition of the plants used in its determination and by the environmental conditions under which it is determined, as well as by the soil texture. Briggs and Shantz (1912) concluded, however, that the soil texture was the only factor materially affecting the moisture content at permanent wilting. Age of the plants did not materially affect the values, as the same results were obtained with seedlings and with well-grown grass plants. Plants grown with different amounts of soil moisture wilted at the same moisture content. This would indicate that drought resistance had not been increased by growing the plants in dry soil. Reaching conclusions contrary to the views previously accepted, they found no important differences between different species of plants in regard to their ability to reduce

the moisture content of the soil before wilting. The differences observed between various species of crop plants were too small to explain differences in drought resistance, and even these small differences were believed to result from differences in root distribution rather than from differences in forces that bring about water absorption. Although the results and conclusions of Briggs and Shantz have been criticized for various reasons, they seem well substantiated by more recent investigations. These investigators found that while all species wilted at approximately the same moisture content in a given soil, there were considerable differences between species in ability to survive in soil below the wilting point. Some species died soon after wilting, while others survived for long periods in a partially wilted condition. Some of the criticism of the work done by Briggs and Shantz probably results from failure to differentiate between the early stage of wilting used by them as an end point and later stages approaching the ultimate wilting point of Taylor, Blaney, and McLaughlin (1934) and of Furr and Reeve (1945).

The type of plant used in determining the wilting percentage does have some bearing on the reliability of the results. The first requirement is a well-developed fibrous-root system that permeates the soil so completely that the moisture content is evenly reduced throughout the soil mass. The leaves must be of a type which show wilting clearly, and plants with heavily cutinized leaves, such as pine needles, are therefore unsatisfactory. Jester, working in the author's laboratory, found that the wilting point of a sandy loam, which was determined simultaneously with oats, black locust, and loblolly pine seedlings, seemed to be highest with oats and lowest with pine seedlings. Probably this does not represent any difference between these species in ability to reduce the moisture content but resulted, rather, from the greater difficulty in determining when the pine seedlings had begun to wilt. In another comparison, Coile and Gaiser (1947) found no difference between the permanent-wilting

percentages determined with loblolly pine and with black locust. Fowells and Kirk (1945) found that *Pinus ponderosa* seedlings reduced the moisture content of a soil to 3.4 per cent before visibly wilting, but that sunflowers wilted in the same soil at a moisture content of about 7 per cent. Moinat (1932) suggests that determination of the wilting point may be in error, because the leaves remove water from the stem or from other parts of the plant after the soil is really at the wilting point. This is a negligible factor when oats or other grasses are used as indicators. It probably is a minor factor also if the wilting process is terminated when the first pair or two of leaves have wilted.

Table 4. Permanent Wilting Percentages of Various Soil Types as Determined with Different Species *

Species	Coarse sand	Fine sand	Sandy loam	Loam	Clay loam
Moisture equivalent....	1.55	5.5	12.0	18.9	27.4
Corn................	1.07	3.1	6.5	9.9	15.5
Sorghum..............	0.94	3.6	5.9	10.0	14.1
Kubanka wheat.......	0.88	3.3	6.3	10.3	14.5
Kherson oats..........	1.07	3.5	5.9	11.1	14.8
Canada field peas......	1.02	3.3	6.9	12.4	16.6
Tomato..............	1.11	3.3	6.9	11.7	15.3
Japanese rice..........	0.96	2.7	5.6	10.1	13.0

* From Miller (1938, p. 194), compiled from data of Briggs and Shantz.

A lively controversy arose concerning the influence of atmospheric factors on determination of the wilting percentage. Briggs and Shantz (1912) made most of their determinations in a greenhouse where transpiration was very moderate but considered that the values were not materially affected by atmospheric conditions, such as humidity, or by moderate changes in light intensity. Brown (1912) found that plants growing in the open wilted at a higher soil-moisture content than did plants growing in shade with a

lower rate of transpiration, and Caldwell (1913) obtained similar results. He concluded that "for a series of plants grown in any one soil and wilted under a number of aerial conditions, as many different soil-moisture contents are obtained as there are sets of conditions." Shive and Livingston (1914) wilted several species under various degrees of shading and reported that the moisture content of the soil at permanent wilting was lowest in the shade and highest in full sun. Veihmeyer and Hendrickson (1934), however, found the wilting percentage of a particular soil to be remarkably constant, regardless of size of container, species of plant, season of the year, or degree of exposure. Sunflower plants were wilted in the spring and during the hot, dry weather of late summer. Some seedlings were allowed to wilt in a moist chamber in a greenhouse, others in a whitewashed greenhouse, and others in the open. The average wilting percentage was the same in all instances, although the rate of evaporation was several times as high when some plants wilted as when others wilted. Furr and Reeve (1945) obtained similar results.

Sachs (1887, page 259) seems to have been the first to study the effect of soil texture on the availability of water to plants. He found that when tobacco wilted in sand, in loam, and in a mixture of humus and sand, the moisture contents at the time of wilting were 1.5, 8.0, and 12.3 per cent, respectively. Apparently little attention was paid to this situation afterward until publication of the very extensive work of Briggs and Shantz (1912). They found the moisture content at permanent wilting to vary from 1 per cent in sand to 25 per cent in clay and to even higher percentages in soils containing much organic matter. The moisture content of a soil at permanent wilting can be determined most reliably by direct observation. Since the term wilting coefficient has often been applied to indirect determinations, it would seem preferable to use the term permanent-wilting percentage, as suggested by Veihmeyer and

Hendrickson (1928), to indicate determinations made by the direct method.

Wilting, of course, does not begin at a specific moisture content, but it does begin within a narrow range of soil moisture for which the value given as the permanent-wilting percentage is the average. According to Hendrickson and Veihmeyer (1945), if care is used, this range need not exceed 0.5 per cent for coarse-textured soils and 1 per cent for fine-textured soils. They have a useful discussion of some of the precautions necessary to obtain reliable results. The more care taken in making the determinations, especially in bringing all plants to the same stage of wilting, the more consistent are the results. Hendrickson and Veihmeyer, who prefer sunflower plants for routine work, state that they do not distinguish between first permanent wilting and ultimate wilting but simply terminate the experiment when permanent wilting of the plants becomes visible. Since the permanent-wilting percentage is so stable for a given soil and since it rather accurately indicates the lower limit of soil moisture available for plant growth, it is perhaps the most important of all soil constants for the plant scientist.

Surface forces, such as those by which water films are held to soil particles, decrease in magnitude with increased temperature. It would therefore be expected that the moisture content of the soil at permanent wilting would be lower in warm than in cool soil. Determinations under laboratory conditions indicate that this is true, but the difference usually is not great enough to be of much practical importance. As an extreme example, Richards and Weaver (1944) found moisture content of a clay soil at a moisture tension of 15 atmospheres to be 20.3 per cent at zero and 14.0 per cent at 37.5°C. The effect of temperature was much less on coarse-textured soils. Hendrickson and Veihmeyer (1945) found that direct determination of permanent-wilting percentage with sunflowers was not affected appreciably by temperatures in the range from about 10 to 40°C., a range seldom exceeded in practice.

Experimental Control of Soil Moisture

Numerous investigations have been made of the effect of soil moisture on plant growth. Not all the investigators did what they supposed they were doing. In the older literature, experiments frequently were described in which plants were said to have been grown in containers maintained at certain moisture contents, as at 10, 20 and 30 per cent of the dry weight of the soil. In other investigations it was claimed that the soil was maintained at optimum, suboptimum, and supraoptimum moisture contents. Engineers have described methods of wetting soil intended for use in construction to some predetermined moisture content by sprinkling a certain amount of water over the surface.

The impossibility of doing these things should have been realized by all who have observed the distribution of moisture in the soil after a rain or who have considered the physical forces acting on soil moisture. Strange to say, however, it was not until comparatively recently that Shantz (1925) and Veihmeyer (1927) called attention to the fact that if a small quantity of water is applied to a mass of dry soil the upper layer is wetted to the field capacity and the remainder of the soil mass remains unwetted. Addition of more water results in wetting the soil to a greater depth, but there will always be a definite line of demarcation between the wetted and the unwetted soil. This situation has been observed by everyone who has dug in soil after a summer shower and observed the well-defined boundary between the wet soil and the dry soil beneath. Since the field capacity is the amount of moisture held against gravity by a soil, it is obviously impossible to wet any soil mass to a moisture content less than its field capacity. If a container is filled with dry soil having a field capacity of 30 per cent and enough water is added to wet the whole mass to 15 per cent, one half of the soil will be wetted to field capacity and the other half will remain dry. Obviously, the earlier investigators did not really maintain their plants at the specified soil-moisture

contents but merely gave them various amounts of water distributed in various proportions of the soil mass used in their experiments.

Numerous investigators have attempted to devise means of controlling the moisture supply and of improving its distribution in the soil for experimental purposes. Livingston (1908, 1918) suggested the use of porous porcelain cones buried in the soil and connected to a reservoir, as a means of controlling the supply of moisture (see Fig. 41). This system became known as the autoirrigation system and the cones as autoirrigators. Livingston and his colleagues attempted to limit the water supply by introducing mercury columns of various heights between the irrigator cones and the reservoir, thus increasing the tension necessary to bring about water movement from reservoir to soil. Unfortunately, there is a tendency for the soil to dry out at a distance from the irrigators. The roots become massed around the irrigators, somewhat nullifying the control, because absorption occurs directly from the surface of the irrigators, rather than from the soil which is supposed to have come into equilibrium with them. An improvement in moisture distribution is afforded by the use of double-walled pots with a space for water between the glazed outer wall and the porous inner wall (Wilson, 1929; Richards and Blood, 1934). The high cost of these containers has prevented extensive use of them. Richards and Loomis (1942) found that double-walled pots maintained a constant soil-moisture content for small plants with low tensions (short mercury columns in the supply tubes), but not for large plants which removed water rapidly. Even with tensions as low as 2 to 4 cm. of mercury, water often was removed faster than it could be supplied. This occurs because water moves so slowly from wet to dry soil.

Emmert and Ball (1933) attempted to maintain moisture contents other than field capacity by dividing the soil in small containers into several layers, each about 2 in. thick. The layers of soil are separated by layers of coarse sand

about 1 in. thick. Water is supplied through tubes, which lead to each layer of sand, ensuring that each soil layer shall receive some of the added water.   Hunter and Kelley (1946a) grew plants in long columns of soil separated into horizons of different moisture contents by partitions made of cloth impregnated with paraffin and road tar. Such partitions are easily penetrated by roots but not by water. Moinat (1943) described a method of maintaining soil in a series of containers at various moisture contents by placing the soil on plaster-of-paris plates on top of sand columns of various heights.   The sand columns stand in free water maintained automatically at a constant level. A variation of this is a framework resembling steps, placed over a large metal pan.   The framework is filled with sand and the pan is kept filled with water. Plants are grown at various levels in pots buried in the sand and those at the top naturally receive less water than those at lower levels, because of their greater distance above the water level.

In most experiments it is desirable to keep the entire soil mass as nearly as possible at the field capacity. If all the water is added to the top, poor distribution often occurs. It is, therefore, desirable to install some sort of water-distributing system, especially in large containers.   This can be accomplished by adding the water through a coil of perforated tubing placed in the soil, by leading a tube to an inverted flower pot located in the center of the soil mass, or by adding the water through columns of fine gravel that extend downward in the soil (Miller, 1938). Such devices probably also improve soil aeration. Several devices have been described for adding water automatically to the soil as it is removed and even for recording the amount added (Johnston and Atkins, 1939; Steinberg, 1930), but these are impractical for large-scale experiments.

In general, it is impracticable to attempt to maintain the moisture content of soil continuously at any value other than saturation, field capacity, or the permanent-wilting percentage. Any attempt to wet the soil mass in a container

to less than field capacity will simply result in a part's being wetted to field capacity while the remainder is left unwatered (Hendrickson and Veihmeyer, 1941). The most practical method of studying the effects of limited water supply on plant growth is to allow the plants to dry the soil in a container to some moisture content well below the field capacity or even approaching the permanent-wilting percentage, before adding water to bring it back up to field capacity. Wadleigh and Ayers (1945) applied this technique to a study of the effects of soil moisture on growth of beans. Plants were grown in 10-gal. containers of soil, which were initially at a moisture content equal to field capacity. The containers were weighed daily, and one group was watered when 40 to 50 per cent of the available water had been absorbed, a second group was watered when 60 to 65 per cent of the moisture had been removed, and the third group was not watered until the plants began to wilt at midday. In all instances, enough water was added at each application to bring the entire soil mass up to field capacity. The minimum moisture contents reached were equivalent to tensions of 250 cm. of water, 750 cm., and approximately 15 atmospheres. Growth of the plants was appreciably reduced by reducing the frequency of watering, and chemical composition was also altered, even in those containers where the soil-moisture content was never allowed to approach the permanent-wilting percentage.

Moisture Control in Greenhouse Practice

Because of the limited soil mass surrounding the roots, potted plants and those growing in greenhouse benches require frequent watering. This is time consuming, and considerable experience is required to avoid under- or overwatering. Surface watering is often uneven, it tends to pack the soil and decrease aeration, and it sometimes causes leaf injury and the spread of disease. Numerous tests indicate that many potted plants grow better when they are supplied with water by some type of autoirrigator than when they are

watered manually. Post and Seeley (1943) described the
use of short pieces of glass rope for supplying water to pot-
ted plants and flats. One end of a piece of the rope is pulled
through the hole in the bottom of a pot and spread out over
the bottom of the soil mass so that it makes good contact
with the soil, while the other end dips into a reservoir of
water. Such devices, of course, maintain the soil at approxi-
mately the field capacity but not at any lower moisture
content. They are particularly useful for house plants,
which usually are either over- or underwatered.

In recent years, attempts have been made to eliminate the
disadvantages of surface watering and to reduce costs by
some more or less automatic control of the water supply.
While the methods devised are still somewhat experimental,
they have been sufficiently successful to indicate that they
will soon be widely adopted on a commercial basis. Some
of them were described by Post and Seeley, and they are
discussed in current periodicals dealing with floriculture and
horticulture. The most common system uses a waterproof
bench with a V-shaped bottom, about 2 in. deep. Half tile
or pieces of eave trough are inverted over the bottom of the
V, which is then filled with a layer of gravel. Pots can be
set directly on a layer of sand placed on top of the gravel, or
the bench can be filled with soil and plants can be grown in
the soil (see Fig. 11). When water is needed, it is run into
the bottom of the V until the gravel is flooded and the soil
above it is wetted by capillarity. The frequency of water-
ing and the amount of water applied can best be determined
by installing a tensiometer. Water usually is applied when
a tension of 5 to 8 cm. of mercury is indicated. Watering
can be made completely automatic by means of a vacuum
gauge connected to a tensiometer and wired through a time
clock so that it will open a solenoid valve in the water line.
When the vacuum gauge indicates the desired tension, it
closes a circuit and the solenoid opens the water line long
enough to run a predetermined amount of water into the
bottom of the bench. In some installations, a constant

water level is maintained in the bottom of the bench by the use of a float valve in a well on the side of the bench. The amount of water supplied can be controlled by the height of the water level and the depth to which the pots are plunged into the sand above the water table.
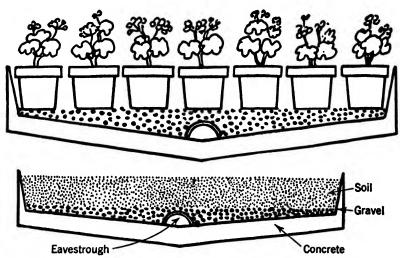

Fɪɢ. 11. V-bottom greenhouse benches arranged for subirrigation, either by automatic or by manual control. Plants may be grown in pots (upper figure) or in soil (lower figure). A constant water level can be maintained in the gravel by installing a float valve in a well on the side of the bench. Intermittent watering can be controlled by the apparatus shown in Fig. 12. (*From Post and Seeley, 1943.*)

Propagating benchęs and wooden benches have been successfully watered by installing glass wicks in the bottom, about 18 in. apart, and allowing them to dip into reservoirs beneath the benches. An ordinary flat of seedlings can be kept automatically watered by a single wick, installed in the center. All these systems depend on capillarity to distribute water through the soil and, after it has once been wetted, they keep the soil approximately at field capacity. Less fertilizer and less water are used than when the plants are watered with a hose and the surplus is allowed to drain off. If evaporation is very heavy, mineral elements tend to

accumulate at the surface with subirrigation systems, but this can be counteracted by surface watering about once a month.
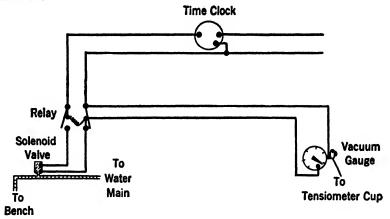
FIG. 12. Wiring diagram for automatic control of the water supply to a greenhouse bench by a vacuum gauge attached to a tensiometer. (*From Post and Seeley, 1943.*)

Irrigation Problems

Irrigation of agricultural land is an example of soil-moisture control on the broadest possible scale. It is by no means so simple a process as is supposed by those who have not studied it in practice. Successful and efficient irrigation involves many problems the solution of which requires some knowledge of engineering, soil-water relations, plant physiology, and the characteristics of the particular crop being grown. A whole book would be required to cover the subject of irrigation thoroughly. The following discussion merely indicates the general nature of the problems.

The major problem is how to maintain sufficient soil moisture for good growth without prolonged saturation of the soil, which is likely to injure the root systems of the crop plants. The land must, therefore, be carefully prepared in order that both high spots, which will be too dry, and low spots, in which plants will be "drowned out," may be eliminated. Development of an efficient distribution system is

an engineering problem, but it is related to soil texture. Longer runs of furrow with less slope can be used on clay soil than on sandy soil, where uneven distribution of water
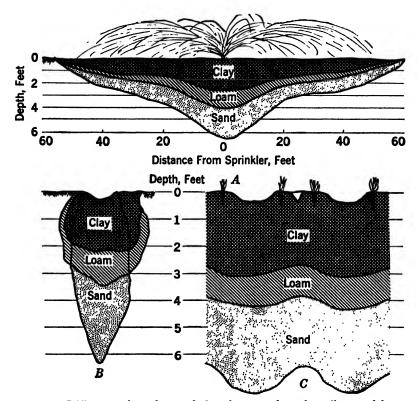
Fig. 13. Differences in volume of clay, loam, and sandy soil wetted by a given volume of water. Since water movement is mainly downward, the furrows must be close enough together and the sprinklers must overlap enough to ensure that all of the soil between them is wetted. (*From Doneen and MacGillivray, 1946.*)

is likely to occur if the runs are too long or if the slope is too gradual. Furrow irrigation is less likely to cause injury to plant roots from poor aeration than is the basin system of irrigation so often used in orchards. Adequate drainage is as important as an adequate supply of water, because inadequate drainage and the resultant waterlogging of the

soil often results in injury to crops from poor aeration and salt accumulation.

The amount of water to be added at one time and the frequency of irrigation depend on the texture and depth of the soil, the depth of rooting of the crop, and its rate of transpiration. As has been indicated earlier in this book, sandy soils must be irrigated more frequently, although they require less water per application than do clay soils. Care must be exercised not to apply too much water to shallow soils underlain by hardpan or by a shallow water table, lest they become waterlogged. Shallow-rooted crops, such as sweet corn, onions, and lettuce, require more frequent irrigation than do such deep-rooted crops as tomatoes, watermelons, and pumpkins. The rate of evaporation from the soil surface and the rate of transpiration also affect the frequency of irrigation, because they determine the rate of removal of water from the soil. Water use is much lower during cool, cloudy weather than during hot, clear weather; and young crops use less water than is needed by older crops, having a larger leaf area. Irrigation should be adjusted accordingly.

According to Doneen and MacGillivray (1946), some crops may suffer considerable reduction in yield from lack of water without exhibiting any conspicuous symptoms. The experienced grower watches his crops closely for such symptoms of an inadequate water supply as wilting or rolling of leaves, change in color, or cessation of growth. The first symptom often is decrease in or cessation of growth of the plant or the fruit, but this can be detected only by careful measurements. Sampling the soil in the root zone to determine its moisture content also gives a reliable indication of the amount of available water. Methods of determining soil-moisture content *in situ* by the use of tensiometers and resistance blocks have been discussed earlier in this chapter. It is believed that such methods will come into more general use in the future.

CHAPTER 5

STRUCTURE AND GROWTH OF ROOTS

With the exception of aquatic plants and a few epiphytes, plants absorb practically all of their water through their roots. It is true that water can be absorbed through the leaves of many mesophytes, but such absorption is of little significance, because conditions are seldom favorable for its occurrence (Brierley, 1934; Miller, 1938; Williams, 1932). The effectiveness of roots as absorbing surfaces depends on the extent of the root systems and on the efficiency of individual roots. The latter depends largely on their anatomical structure, which is modified considerably during growth. The characteristics of a root system depend partly on its heredity and partly on the environment in which it develops. This chapter deals principally with the structure and growth of roots. The various factors affecting the rate and amount of root growth will be discussed in Chap. 6.

Primary Growth of Roots

During growth and maturation, roots undergo extensive anatomical changes that affect their permeability to water and solutes to a marked extent. Growing roots usually are considered to possess four distinct regions—the root cap, the meristematic region, the region of cell elongation, and the region of differentiation and maturation; but in at least some roots these regions are by no means so clearly defined as is often supposed. While the root cap is usually well defined, it is absent from certain roots, such as the short roots of pines. It is composed of very loosely arranged cells and probably has no effect on absorption.

The meristematic region typically consists of numerous

small, compactly arranged, thin-walled cells, almost completely filled with cytoplasm. Relatively little water is absorbed through these cells. It is possible that this is partly because of the resistance offered by the dense cytoplasm and partly because the cells of this region develop a higher diffusion-pressure deficit than do cells farther back in the root. The elongation of roots of *Phleum pratense* has been described by Goodwin and Stepka (1945). If the meristematic region is defined as that region in which transverse cell divisions are occurring, it includes the apical 425 microns of the root, exclusive of the root cap. Goodwin and Stepka found this to be divided roughly into two parts. The apical 200 to 300 microns consist of small cells with tiny vacuoles, which divide and elongate slowly, while the basal portion is characterized by rapid cell division, increase in size of vacuoles, and cell elongation, so that root elongation is much more rapid in this region than in any other part of the root. Growth in the apical portion of the meristem probably is limited by food supply, as the phloem is not differentiated any closer than 230 microns from the apex and food must move the remainder of the distance across undifferentiated cells. From about 400 to 1,000 microns back of the root apex, slow root elongation occurs as the result of cell elongation, little or no division occurring in this region.

It is impossible to delimit a definite zone of differentiation, because different types of cells are differentiated at different distances behind the root apex. Thus in Phleum, sieve tubes mature within 230 microns of the apex, well within the meristematic zone, while xylem elements first become differentiated about 1,000 microns behind the apex. Phloem also becomes differentiated sooner than xylem in the roots of Valencia orange (Hayward and Long, 1942) and in pear roots (Esau, 1943). Furthermore, the rate of root elongation has some bearing on the location of these zones, because in slowly growing roots differentiation of tissues extends closer to the root tips than it does in rapidly growing roots; and when growth is checked or ceases, differentiation usu-

ally extends almost to the apex, only a small meristematic region being left. Neither Brumfield (1942) nor Goodwin and Stepka found evidence of rhythmic elongation, but it has been observed by Friesner (1920) and others to occur in the roots of several species.

Burstrom (1947) found cell division and cell elongation to be somewhat independent of each other, so that root elongation might be controlled largely either by the rate of cell division or by the rate of cell elongation. A high concentration of phosphorus promoted cell division but had little effect on cell elongation, while nitrates increased the amount of cell elongation but did not affect the rate of cell division.

Supported behind by the older, more rigid tissue, and on the sides by soil particles, the root tip is pushed forward through the soil by the elongating cells, sometimes at rates of 5 cm. or more per day. Usually its course is somewhat tortuous, as it follows the path of least resistance between soil particles and around pebbles and other obstacles. Although cells of the root cap are torn off by contact with soil particles, they are replaced by new ones formed at the apex of the meristematic zone.

Very considerable pressures are developed by elongating and enlarging roots, as is evidenced by the lifting of sidewalks and cracking of masonry walls. If it be assumed that the root cells develop an average turgor pressure of only 5 atmospheres, then the roots might exert a pressure of 75 lb. per sq. in. or over 5 tons per sq. ft. of surface. Clark (1875) gave a number of examples of the force exerted by growing roots and, as evidence of the pressure developed by enlarging plant tissue, reported an experiment in which a growing squash fruit supported a weight of 5,000 lb.

As the newly formed, thin-walled cells at the base of the zone of cell enlargement lose their ability to elongate, they become differentiated into the epidermis, cortex, and stele, which constitute the primary structure of a root.

Roots differ from stems by having a relatively smaller

stele and larger cortex, and the conductive tissues usually form a solid mass in the center instead of being scattered in bundles around the periphery of a central pith, as in most stems; but a pith sometimes occurs. The primary xylem usually consists of several strands arranged radially, with strands of phloem located in the angles that they form. The narrow layer of parenchyma cells surrounding the xylem and separating it from the phloem later becomes the cambium and produces the secondary xylem and phloem. The outermost layer of the stele, adjacent to the endodermis, is the pericycle. Its cells retain their ability to divide and not only give rise to branch roots, but later, during secondary growth, usually produce the cork cambium found in older roots.

The endodermis, as a rule, is a single layer of cells, but it sometimes consists of two layers, or even of groups of cells. According to Williams (1947), the endodermis at first behaves like a cambium and produces all the cortical tissue before differentiating into the cylinder of cells that is characteristic of the mature region of most roots. Early in its development, suberized or cutinized thickenings, called Casparian strips, develop on the radial and end walls of many of the endodermal cells, rendering them impermeable to water. As the endodermis matures, the inner tangential walls, as well as the radial and end walls, sometimes become much thickened and lignified. Priestley (1920) claimed that the impermeable radial walls of the endodermal cells have important effects on absorption of water and on the development of root pressure, because they force all water and solutes to move through the protoplasts. This seems doubtful, because the cells opposite the xylem points, known as passage cells, usually remain thin-walled and appear to afford a path for free movement of water and solutes. Breaks in the endodermis, permitting the entrance of water and solutes, probably also are provided by root initials, which usually have developed by the time the endodermis has matured (Steward, Prevot, and Harrison, 1942). The physiological

importance of the endodermis seems to have been over-emphasized. Between the endodermis and epidermis are usually 10 to 20 layers of parenchyma cells. Generally these are arranged loosely, with large intercellular spaces. A cross section of a young root is shown in Fig. 14.

Root Hair Cell
Epidermis
Cortex

Phloem
Endodermis
Pericycle
Xylem
Casparian Strip
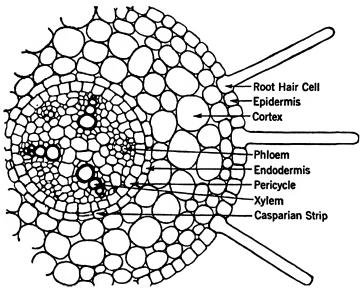
Fɪɢ. 14. Semidiagrammatic view of a transverse section through a squash root in the region where maximum water absorption occurs. (*From Crafts and Broyer, 1938.*)

Epidermis and Root Hairs

The epidermis is composed of thin-walled, elongated cells, which are often slightly smaller than the cortical parenchyma cells. Sometimes a second layer of cells, the hypodermis, lies within the epidermis. Usually as the epidermis matures the cell walls become suberized and, consequently, less permeable to water. The most distinctive characteristic of the root epidermis is the production of root hairs, which usually arise as protrusions from the external, lateral cell walls, though in a few species, including those of citrus and pine, they sometimes arise from cortical cells one or two

layers beneath the epidermis.   In some species, any or all the epidermal cells can produce root hairs, but in other species the rudimentary epidermal cells divide, giving rise to long epidermal cells and to short ones known as trichoblasts, which usually produce the root hairs (Sinnott, 1939; Sinnott and Bloch, 1939).   The morphological differentiation between trichoblasts and other epidermal cells three or four times as long is said to be quite definite in some species, less definite in others, and absent in still others (Cormack, 1944). In cabbage, rows of short and long cells alternate, while, in Phleum, long and short cells occur alternately in the same row and, in tomato, only long cells occur.   Furthermore, while root hairs are usually produced by the short cells, or trichoblasts, these hairs, under favorable conditions, are produced by long cells also (Cormack, 1945).

The walls of young epidermal cells consist of an inner layer of cellulose and an outer layer of pectic material, probably pectic acid (Cormack, 1935; 1944).   These walls are readily extensible; as the vacuoles increase in size and as turgor pressure develops, rapid elongation occurs.   According to Cormack, if sufficient soluble calcium is present and the pH is favorable (pH 6 to 9 for *Phleum pratense*), the soft pectic acid of the side walls is gradually converted into rigid calcium pectate, with the resultant slowing down and finally the stopping of cell elongation.   If vacuolation is occurring rapidly at the same time and if sufficient turgor pressure is developed, the softest portion of the cell wall is bulged outward, forming a root hair.   Apparently, the walls of epidermal cells are slower in maturing at the apical end than at the basal end, hence the root hairs develop at the apical end rather than at the basal end, where the wall has already become relatively firm and inextensible.   Possibly when root hairs occur near the middle of epidermal cells, as in Sporobolus, it is an indication that cell elongation occurred after the root hairs began to develop (Cormack, 1944; 1945).   Another explanation offered for the typically distal location of the root hairs of many species is that their posi-

tion is determined by the distribution of materials under control of cell polarity (Sinnott and Bloch, 1939). If insufficient calcium is present or if the medium is too acid for formation of calcium pectate, either no root hairs are formed or any that may be formed are distorted. If an excess of calcium is present, the walls harden too rapidly to permit normal root-hair formation. If the walls harden too slowly, the cell will continue to elongate rather than to produce root hairs; if the walls harden too rapidly, no root hairs will be produced.

While the development of root hairs is more or less affected by pH, by the kind and the concentration of ions, by aeration, by temperature, and even by light, there is so much difference between species that generalizations are difficult. It can be stated, however, that most land plants produce the maximum number of root hairs in well-aerated soil having a moisture content between the permanent-wilting percentage and the field capacity, and that their development is inhibited in both dry and saturated soil and by an excess of salts (Hayward and Blair, 1942). Elodea will produce root hairs in water as abundantly as it does in soil, if the roots are kept in darkness. Apparently, in the light a layer of cutin is produced which hinders root-hair formation (Cormack, 1937). Extensive discussion of the factors affecting root-hair formation is somewhat academic from the standpoint of the success of plants under field conditions. If the soil is too dry or too wet, or if the concentration of salts is too high for root hairs to develop, plant growth is likely to be seriously hindered, for reasons quite independent of the absence of root hairs.

According to Miller (1938), root hairs vary in length from a mere protuberance to about 10 mm. and have an average diameter of about 10 microns. The root hairs of winter rye (*Secale cereale*) studied by Dittmer (1937) were 0.7 to 1.0 mm. in length and 12 to 15 microns in diameter. Winter-rye plants grown in boxes of soil in the greenhouse produced an average of 14 billion root hairs per plant, with a

total surface of 4,321 sq. ft., or 1.6 times the surface of the roots themselves. Schwarz (Miller, 1938, page 151) reported that root hairs increased the absorbing surface of corn sixfold and that of peas twelvefold. These measurements were made on roots grown in moist air; it seems possible that the number and length of root hairs is greater on roots grown in moist air than on roots grown in soil. Evans (1938) stated that, although root hairs increase the absorbing surface of one variety of sugar cane only 3.2 times under field conditions, so many are produced in moist air that they increase the surface 8 to 10 times. Root hairs are more abundant on grasses than on most other species and, under field conditions, they are said to be rare on peanuts (Reed, 1924). They are absent on certain conifers (Busgen and Munch, 1926) and on pecan (Woodroof and Woodroof, 1934). Absence of them on many forest trees probably is the result of extensive development of mycorhizae. Roots of 7-week-old black-locust seedlings, grown in fertile soil in the greenhouse and studied by Scholtes in the author's laboratory, possessed 520 root hairs per square centimeter of root surface, while loblolly pine roots of the same age and grown under the same conditions bore only 217 root hairs per square centimeter (Kozlowski and Scholtes, 1948). These numbers are a decided contrast to those for winter rye, with about 2,500 root hairs per square centimeter on the primary roots. Nutman (1934) reported that root hairs of *Coffea arabica* increase the absorbing surfaces on which they are produced about 8.5 times. There are undoubtedly hereditary differences between species with respect to numbers of root hairs per unit of root surface, as well as differences caused by environmental factors.

Root hairs are usually assumed to be short-lived, being destroyed in a few days or weeks by the changes associated with secondary thickening, such as suberization or lignification of epidermis or hypodermis. This is not always true, however, as even the oldest roots of the 4-month-old rye plants studied by Dittmer possessed healthy root hairs.

Weaver (1925) found that root hairs of winter wheat growing out of doors in the autumn did not begin to die until the roots were 7 weeks old, and most of them were alive after 10 weeks. On some species, the root hairs may become suberized or lignified and persist for months or even for years. Persistent root hairs have been observed on Valencia orange seedlings (Hayward and Long, 1942), Cercis, Gleditsia, and Gymnocladus (McDougall, 1921), members of the Commelinaceae (Pinkerton, 1936), sugar cane (Evans, 1938), and *Dionaea muscipula* (Shunk, 1940); and root hairs 3 years old were reported to occur on certain composites (Whitaker, 1923). It is questionable if such root hairs are of importance in the absorption of water and solutes, though Muller (1946) reported that old root hairs of guayule (*Parthenium argentatum*), empty of cytoplasm, absorbed water when brought into contact with it.

Secondary Growth

Secondary growth generally destroys the epidermis and the root hairs. Sometimes the hypodermal cells become suberized and a cork cambium (phellogen) develops in the outer part of the cortex. In the roots of Valencia orange and some other species, the hypodermal cells sometimes produce secondary root hairs, lenticels, and absorbing areas consisting of groups of thin-walled, radially elongated cells (Hayward and Long, 1942). Water presumably is absorbed through all these structures. Usually, as cambial activity increases the diameter of the stele, the cortex and epidermis are split off and disappear. Frequently, a cork cambium arises from the pericycle and the roots become covered with a thin layer of corky tissue containing numerous lenticels. In woody roots, successive cork cambiums usually develop until the cortex has disappeared; so the arrangement of tissues in large, woody roots becomes essentially similar to that in woody stems. Apparently, however, the bark of roots is considerably more permeable to water than is the bark of stems.

The Absorbing Zone

The review of root anatomy just presented suggests that the chief absorbing zone would be in the younger regions of a root—a conclusion which is supported by extensive experimental evidence. Although Coupin (1919) believed that absorption occurred chiefly through the root tips, it is generally agreed that little or no water is absorbed through the root cap and the meristematic region (Brewig, 1936*b*; Hayward and Spurr, 1943; Priestley and Tupper-Carey, 1922; Rosene, 1937; Sierp and Brewig, 1935). According to Prevot and Steward (1936) and Steward, Prevot, and Harrison (1942), the potential absorbing zone for salts, and presumably for water, of barley roots grown in water culture extends from the tip back to the region where branch roots develop; but accumulation of salts is greatest near the tip. Rate of respiration also is greatest in the apical centimeter of the root and decreases with distance for several centimeters behind the tip. This was established for *Vicia faba* by Gregory and Woodford (1939) and for barley by Machlis (1944). This gradient may result from a greater amount of protoplasm per unit of root volume, or from a greater rate of respiration per unit of protoplasm near the tip, or from a combination of the two causes. Absorption of water probably is limited in the older regions by increasing suberization of the endodermis, even though the epidermis remains unsuberized. The exact location of the zone of most rapid absorption varies with the age and length of the roots and with the tension developed in the conducting system by the transpiring shoots (see Fig. 15).

Maximum absorption by onion roots, to which micropotometers were attached at various distances back of the tips, occurred in regions 40 to 60 mm. back of the tips in roots more than 70 mm. long and decreased from this region toward both tip and base of root. In younger roots, less than 50 mm. in length, there was greater absorption toward the base than toward the tip (Rosene, 1937). Absorption

by corn roots was found to increase to a maximum about
10 cm. back of the root tip and then to decrease toward the
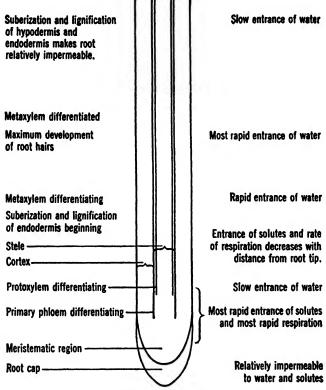
FIG. 15. Diagram of a young root, showing relation between anatomy and
absorbing regions for water and solutes. The relative locations of these
regions are similar in all roots, but the distance from root apex to a region
showing a given degree of differentiation varies widely with the species
and the condition under which the root is grown. The stages in differentia-
tion and the location of the region of maximum water absorption are based
principally on a study of corn roots by Hayward and Spurr (1943). The
location of the region of maximum accumulation of solutes is based on
studies of barley roots by Steward, Prevot, and Harrison (1942). The
region of most rapid respiration is located on the basis of a study of
barley roots by Machlis (1944).

base in roots more than 10 cm. long (Hayward, Blair, and
Skaling, 1942). It has been observed that the zone of most
rapid absorption of *Vicia faba* roots is a few centimeters

back of the root tip, with absorption decreasing both apically and basally from this zone. When the shoot is transpiring rapidly, the absorbing zone is extended, including the entire unbranched region of Vicia roots (Brewig, 1936a). This has been attributed to changes in permeability produced by increased tension in the xylem, but it seems more probable that the increased tension in the xylem merely causes water intake through tissues that offer too high a resistance to water movement to permit measurable passage at lower pressure gradients. It has also been observed that removal of part of the roots may result in increased rate of absorption through the remaining roots if the rate of water loss from the shoot is high (Rosene, 1937). According to Hayward and Spurr (1943), the absorbing zone depends on the histological development of the root, maximum absorption occurring from the point where the xylem is fully matured to the level at which permeability is reduced by suberization and lignification of the epidermal and the hypodermal cells. In general, it appears that the region of maximum permeability to water corresponds approximately with the region in which root hairs are normally developed (see Fig. 15).

Since absorption occurs most readily near the root tips, plants that have much-branched roots and numerous tips ought to possess a considerable advantage over those that have sparse branching, especially when the soil is dry. Sorghum is considerably more drought resistant than corn. Miller (1916) attributed this to the fact that, while sorghum has a smaller leaf surface than corn, it has twice as many secondary roots, and so, a more effective absorbing system.

It has long been assumed that root hairs materially increase the absorbing surface in contact with the soil. It was only recently, however, that actual measurements of absorption through root hairs were made by Rosene (1943). These indicate that water is absorbed at about the same velocity per unit of surface through root hairs of radish as

through the hairless epidermal cells of onion. Hohn (1934) concluded that root hairs do not significantly increase the absorption of water by roots in water or in culture solutions. This probably is true, since it seems likely that absorption from water, dilute solutions, or soils more moist than their field capacity is limited not by the epidermal surface in contact with the liquid, but by internal factors, such as the tension in the xylem, the capacity of the conductive system to remove water, or the permeability of the root tissues. In soil below the field capacity, extent of root surface in contact with the soil particles is of greater importance, because the water in capillary films around the soil particles moves very slowly and is immediately available only to those roots which come into actual contact with the soil particles.

The importance of root hairs in making water available is illustrated by data from a study of the root systems of winter rye plants made by Dittmer (1937). The tertiary and quaternary roots of these plants averaged 125 microns in diameter. A segment of such root 1 m. in length, but lacking root hairs, would have a surface of only 3.92 sq. cm. in contact with the soil. Water would be absorbed readily from only a thin layer of soil, 1 mm. or less in diameter, immediately surrounding the root. Such a layer would have a volume of about 0.785 cc., including the root. Actually, these roots possess numerous root hairs, averaging 800 microns in length. These enable the root to come into contact with a cylinder of soil about 2 mm. in diameter, having a volume of 3.14 cc. Thus the root hairs on the roots of rye more than double the surface through which absorption can occur and quadruple the volume of soil from which water can be absorbed.

Absorption by Older Roots

At times when the soil is cold or dry or when the concentration of the soil solution is too high, root elongation is very slow or ceases completely, and few or no unsuberized root tips can be found. McQuilkin (1935) reported that

growing root tips are rare on *Pinus rigida* in July, August, and September, and that many root tips die during the drier part of the summer. Most roots were becoming suberized to the tips just when an extensive absorbing system seemed most necessary. Reed (1939) found very little root elongation in loblolly- and shortleaf pine roots during the coldest part of the winter and during dry periods in the summer, when soil moisture approached the permanent-wilting percentage. It is also reported that few or no white, unsuberized root tips can be found on citrus trees during the winter (Chapman and Parker, 1942; Hayward, Blair and Skaling, 1942; Reed and MacDougal, 1937). These and other evergreen species are obviously losing considerable quantities of water by transpiration and therefore, presumably, must be absorbing equivalent quantities through the suberized portions of their roots. Crider (1933) and Nightingale (1935) also have reported instances where woody plants possessing no actively growing roots were nevertheless able to absorb water and even minerals through their suberized roots.

No actual measurements of absorption were made until recently, when it was found by Hayward, Blair and Skaling (1942) that measurable quantities of water are absorbed through the suberized roots of sour-orange seedlings. Kramer (1946) found surprisingly high rates of absorption from potometers attached to suberized roots of small shortleaf pines growing in the open. Suberized roots of yellow poplar and dogwood also were found to be quite permeable to water. According to Addoms (1946), entrance of water occurs chiefly through lenticels, breaks around branch roots, and wounds in the bark. It appears likely that sufficient water can be absorbed through a completely suberized root system to replace moderate transpiration losses. When the growing, unsuberized tips constitute only a small proportion of the root surface, as in many woody species, even in the summer, absorption through the suberized portions must be of considerable importance. Dead roots also can function

as absorbing surfaces, as long as they are not destroyed or plugged up by the activities of microorganisms. In fact, dead roots offer much less resistance to the absorption of water than do living roots (Kramer, 1933).

Mycorhizae

The root systems and absorbing surfaces of most forest trees and shrubs, as well as those of some herbaceous species, are considerably modified by the presence of mycorhizae. These structures are formed as a result of the invasion of young roots by hyphae of various species of fungi commonly found in forest soils. Two principal types occur, endotrophic mycorhizae, in which the mycelium develops principally within the cortical cells and only individual hyphae appear at the surface, and ectotrophic mycorhizae, in which the mycelium penetrates between the cortical cells, separating them from each other and producing marked hypertrophy of the roots. Combinations of these two types often occur also. A feltlike covering, or mantle, of mycelium one to several layers of hyphae in thickness is also produced over the surface of the roots. According to Hatch and Doak (1933) and Hatch (1937), the type of root system determines the type of mycorhizae developed. Trees with roots that can be differentiated only as coarse and fine roots have endotrophic mycorhizae.

Trees of the Abietineae, Salicaceae, Betulaceae, Fagaceae, Hicoria, and a few others have two distinct types of roots—long roots and short roots. Long roots include tap roots, laterals called "mother roots," and continuations of mother roots called "pioneers." The mother roots elongate moderately rapidly and produce numerous short roots that lack root caps, elongate slowly, have few root hairs and those from the epidermis, branch dichotomously, have no secondary growth, and live but one season. Long roots have root caps, produce root hairs from the second or third layer of cortical cells, branch racemosely, exhibit secondary growth, and are long lived. Hatch and Doak assumed that absorption by
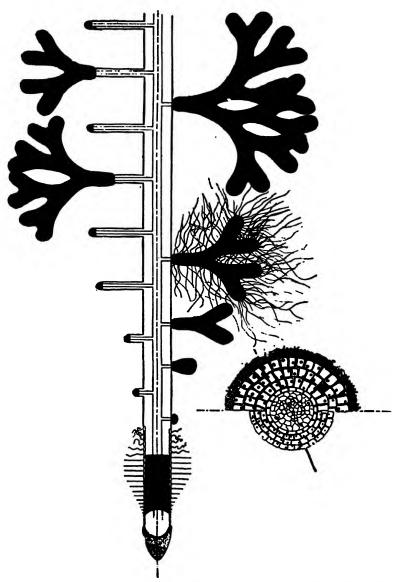
Fig. 16. Development of mycorhizae on a pine root. Solid black areas indicate absorbing surfaces. The main axis is a mother root bearing a root cap and root hairs on the unsuberized surface behind the meristematic region. On the upper surface is shown the development of mycorhizal branches from short roots. On the lower surface are two mycorhizal branches and several nonmycorhizal short roots. The cross section above represents a mycorhizal root; that below, an uninfected root. (*From Hatch, 1937.*)

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long roots would be restricted to the tips, where the conducting system has not yet become differentiated, because development of an endodermis a short distance back of the tips presumably would prevent the entrance of water. It was found later, however, that seedlings bearing only long roots grew well in sand cultures adequately supplied with water and minerals (Addoms, 1937; Hatch, 1937). This constitutes further evidence that appreciable absorption can occur through the suberized surfaces of the older roots. Long roots are seldom converted into mycorhizae, possibly because they elongate too rapidly. Most, or perhaps all, of the laterals grow very slowly, forming typical short roots, which become infected with fungi and develop into mycorhizae. According to Roberts (1948), the mycorhizal roots of *Pinus taeda* have a surface about equal to that of the nonmycorhizal roots. Hatch and Doak claim that they have rarely observed, either in America or in Scandinavia, short roots on forest trees growing in good, acid forest soil which were not mycorhizal, and it has been reported from Germany that all short roots of trees in that country become mycorhizae. According to Hatch, occasionally a profuse surface growth of nonmycorhizal fungi on roots has caused them to be mistaken for true mycorhizae.

There has been considerable controversy as to whether or not mycorhizae are essential to the plants on which they occur. It seems that these fungi are of real importance under natural conditions, although probably under certain conditions most, or perhaps all, plants can be grown without their being present. Hatch (1937) and Mitchell, Finn, and Rosendahl (1937) consider them to be essential to forest trees, because they increase enormously the absorbing surface of the root system. This increase in surface is most important in infertile soils, where the concentration of nutrients is very low. The prevalence of mycorhizae is inversely proportional to the availability of the mineral elements used in growth, as their development is favored by deficiency of nitrogen, phosphorus, potassium, or calcium,

or by lack of balance between these. Conifers grown in infertile soil lacking the fungi necessary to form mycorhizae are very low in mineral content compared to those that grow in soil inoculated with suitable fungi. Some of these conifers actually die, apparently from mineral deficiency.

It has been suggested that failure of conifer seedlings to thrive in nurseries on soil not previously forested often may be caused by lack of fungi to form mycorhizae; and that failure of plantations may occur because the mycorhizae on nursery-grown seedlings are incapable of surviving on sites where the seedlings are afterward planted. Rayner and Neilson-Jones (1944) claim that failure of pines on certain English heath soils is caused by inhibition of mycorhizal development, resulting from low oxygen concentration and presence of toxic substances of biological origin. Björkman (1942) suggested that mycorhizal development depends on a surplus of carbohydrates in the roots. If an abundance of nitrogen and phosphorus is available, carbohydrates are used in growth, little surplus exists in the roots, and fungal growth is retarded. If a moderate deficiency of nitrogen or phosphorus exists, plant growth is retarded and carbohydrates accumulate in the roots in sufficient quantity for abundant mycorhizal development to occur. If the mineral deficiency is too serious or if the light intensity is so low as to decrease photosynthesis seriously, no surplus of carbohydrates occurs and mycorhizal development is retarded.

Hatch regards the ability of the mycorhizal fungi to utilize the complex organic compounds found in forest soils as distinctly secondary to their high absorbing capacity, which results from the high ratio of their surface to their volume. It is suggested by Routien and Dawson (1943) that the greater growth of seedlings bearing mycorhizae is caused by increased salt absorption that results from the increased supply of hydrogen ions provided by the rapidly respiring roots. McComb and Griffith (1946) also attribute the stimulating effect of mycorhizae to their high rate of metabolism and the transfer of growth substances and phos-

phorus from the fungus to the seedlings. MacDougal and Dufrenoy (1944, 1946) consider the synthetic activities of mycorhizal fungi to be very important and suggest that the fungi supply vitamins, nitrogen compounds, and carbohydrates to the plants on which they are growing. Further investigation is needed to establish the importance of this role, but the vital importance of mycorhizae in increasing the absorbing surface and the intake of minerals in infertile soil seems to be adequately established.

Extent of Root Systems

Since the most efficient zone of absorption is usually near the root tip, the number of tips is an important factor in absorption. Because capillary movement of water in soils below field capacity is very slow, continual extension of roots through the soil is essential to the absorption of water and minerals. As was indicated in Chap. 2, water in those areas of soil not penetrated by roots is relatively unavailable to plants, hence those plants which develop the most extensively branched and the most deeply penetrating root systems are best able to obtain large quantities of water and minerals. Busgen and Munch (1926) cite Nobbe as stating that the ability of pine to succeed where silver fir and spruce failed is the result of the pine's possessing 24 times as many branches and root tips as the other species and 8 times the absorbing surface that they have. Realization of the importance of roots in absorption and anchorage has resulted in numerous investigations. Some of the outstanding work on crop plants, grasses, and other herbaceous species is by Weaver and his coworkers. For more detailed discussions and bibliographies the reader is referred to their publications; also to the summary in Miller's text (Weaver, 1919, 1920; Weaver, Jean, and Crist, 1922; Weaver and Bruner, 1927; Weaver and Clements, 1938; Miller, 1938). Among the more recent studies of root development are those of McQuilkin (1935) on pitch pine, Preston (1942) on lodgepole pine, and Muller (1946) on guayule.

The first measurements of root systems known to the author were made by Hales (1727). He estimated that a sunflower plant has 1,448 ft. of roots, with a surface of 2,286 sq. in., while a cabbage plant has only 470 ft. of roots, with a surface of 256 sq. in. After the middle of the nineteenth century, Nobbe, in Germany, made extensive studies of root systems. W. S. Clark (1875) seems to have made the first study in this country, reporting that a squash vine growing in a greenhouse bench possessed 84,000 ft. (15.9 miles) of roots, of which he estimated that 50,000 ft. had been added at the rate of 1,000 ft. a day. The accuracy of these measurements has been questioned by some writers, but the most recent work indicates that Clark's data are not unreasonable. The number and extent of branching of roots is particularly large in grasses. A wheat plant grown without competition developed 44 miles of roots; a spring rye plant, 49 miles; and a plant of wild oats (*Avena fatua*), 54 miles (Pavlychenko, 1937*a*). The roots of corn, sorghum, and other annual crop plants are said to penetrate to a depth of 5 to 8 ft., wherever moisture and aeration permit. Miller (1916) found that the roots of a single corn or sorghum plant among those growing in rows 44 in. apart occupied a cylinder of soil 7 ft. in diameter and 6 ft. deep.

Roots of perennial plants often penetrate to much greater depths, alfalfa having been observed to absorb water from a depth of 33 ft. Frazier (1944) found that the roots of *Apocynum cannabinum* penetrated in one growing season to a depth of 7 ft., with a spread of 12 ft. Wiggans (1936) reports that roots of 18-year-old apple trees in a deep loess soil in Nebraska had penetrated to a depth of over 30 ft. and fully occupied the area between the rows, which were 33 ft. apart. Proebsting (1943) studied root distribution of apricot, almond, cherry, peach, pear, and prune on a deep, sandy loam soil at Davis, California. Very few roots occurred in the surface foot of soil, and the maximum concentration of roots was from 2 to 5 ft., while many roots probably penetrate 15 ft. or more. It should be remembered

that such deep penetration by roots occurs only in relatively coarse-textured, well-drained, and well-aerated soils—never in heavy clay or where a heavy subsoil, a hardpan layer, or
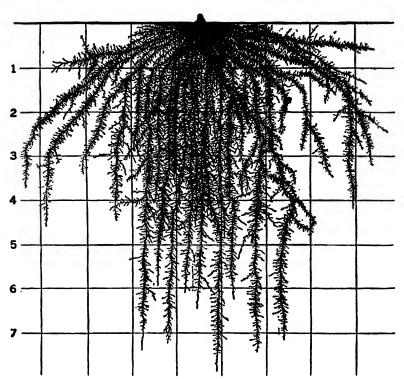
Fig. 17. The root system of a mature corn plant. Note both the spread of roots and the extensive branching, which provides the maximum number of absorbing root tips. This root system was developed in a silt loam soil underlain by well-aerated loess soil many feet deep. Where the subsoil is heavy and poorly aerated, roots do not penetrate so deeply. (*From Weaver, Jean, and Crist, 1922.*)

a shallow water table exists. In contrast to the deep rooting of apples in Nebraska and of other fruits in California, pears growing on a heavy adobe soil in Oregon developed, out of all the roots occurring in the upper 4 ft. of soil, 35 per cent in the surface foot, 68 per cent in the upper 2 ft., and 89 per cent in the upper 3 ft., with only 11 per cent in the 3- to 4-ft. horizon. Absorption of water by these trees was

proportional to the concentration of roots at various depths. Russell (1917), from his experience with the heavy soils of England wrote, "only the upper 6 or 8 in. of the soil is suited to plant life, and the subsoil plays only an indirect part in plant nutrition." In contrast, Miller (1916) found that corn and sorghum could mature crops of grain when the upper 2 ft. of soil were below the wilting coefficient and water was being absorbed from as deep as 6 ft.; while Weaver, Jean, and Crist (1922) proved experimentally that various crop plants can absorb water and nitrates from depths of 2.5 to 5 ft. Doneen and MacGillivray (1946) present evidence that such deep-rooted plants as cantaloupe, pumpkin, and tomato absorb water from depths of 3 to 6 ft., or more (see Figs. 28 and 29).

The extent of the branching and rebranching of root systems, particularly those of grasses, is truly remarkable. Pavlychenko (1937b) found that a 2-year-old plant of crested wheat grass possessed 315 miles of roots, distributed through a soil mass 7 ft. deep by 4 ft. square. Dittmer (1937) estimated that there were 387 miles of roots on a winter rye plant grown for 4 months in a box of soil only 12 in. square by 22 in. deep. This plant bore more than 13 million roots, with a total surface of 2,554 sq. ft., and on these roots were 14 billion root hairs, with a total surface of 4,321 sq. ft. The surface of the aboveground parts of this plant was only 51.38 sq. ft.; hence the root surface, excluding root hairs, was about 50 times as great as the shoot surface. An average of 3.1 miles of roots must have been added daily to produce so extensive a root system. Kramer and Coile (1940) calculated the volume of water made available each day by root growth. It was estimated that the roots and the root hairs came into contact with the soil in a cylinder 2 mm. in diameter. Assuming that 3.1 miles of roots were added daily, this would make available 1.6 liters of water in a sandy loam soil and 2.9 liters from a heavy clay, on the assumption that the soils were initially at field capacity. The new roots produced each day would, there-

fore, have been able to absorb enough water to replace that lost by transpiration. Dittmer (1938) measured the number of roots produced by other species and reported that a cubic inch of soil under oats contained 3.5 ft. of roots; under rye, 5.0 ft.; and under bluegrass, 30 ft., with external surfaces of 15, 30, and 65 sq. in., respectively.

While the roots of woody plants are not usually so much branched as are those of grasses, the concentration of roots under a mature forest stand is quite high. Coile (1937), who studied this in Piedmont forests, found that, per square foot of trench face in the top 5 in. of an oak forest, there were as many as 250 roots less than 0.1 in. in diameter, or more than 90 per cent of all roots of that size class which occurred to a depth of 36 in. In a 35-year-old loblolly pine stand, there were about 160 small roots per square foot of trench face in the top 5 in., again more than 90 per cent of all roots of this size. Nutman (1934) studied the root system of 3-year-old *Coffea arabica* trees growing in the open. He found that 80 per cent of the roots were in a cylinder of soil 5 ft. deep with a radius of 3.5 ft. from the tree trunk, and that this cylinder of soil contained an average of 22,675 meters of roots, equivalent to about 118 m. per cu. ft. of soil. Roberts (1948), in contrast, found only slightly over 21 m. of roots per cubic foot of soil in the A horizon under a 20-year-old loblolly pine stand. It is common for roots of trees to extend out two or three times the radius of the branches, although the region of maximum concentration of absorbing roots is, as a rule, probably under the periphery of the crown.

While the discussion thus far has emphasized the role of roots in the absorption of water, it must not be forgotten that they are equally important in the absorption of minerals. For a long time it was assumed that all absorption of minerals occurred from the soil solution, but in recent years it has been suggested that much mineral absorption occurs by direct contact between the roots and the soil particles (Jenny and Overstreet, 1939). If this is true, then contact

between soil and roots is even more essential for the absorption of minerals than for the absorption of water.

Effect of Roots on Soil

Root systems are important not only as absorbing organs but also in their effects on soil structure and in preventing erosion. Grassland soil is notable for its excellent crumb structure, the result of a high degree of aggregation of the individual particles of the soil. After a few years of cultivation, it often begins to lose its granular structure and, as the crumbs disintegrate, the noncapillary pore space decreases, the water-absorbing and water-holding capacity is reduced, its fertility decreases, and the ease with which water and wind erosion occurs is greatly increased. If such soil is returned to grass for a few years, the soil structure can be greatly improved (Bradfield, 1931; Jacks, 1944; Weaver and Zink, 1946b; Wilson and Browning, 1946). The importance of roots in reducing damage from erosion is generally appreciated. Grasses are particularly effective in holding soil, because of the tremendous number of fine roots produced near the surface (Dittmer, 1938; Weaver and Noll, 1935). The roots hold the soil, while the tops decrease runoff. Even weeds help to hold soil. The importance of forest cover in protecting watersheds from erosion has been widely publicized. Weaver and Zink (1946b) estimated that big bluestem (*Andropogon furcatus*) produces nearly 5.5 tons of roots per acre in 3 years; little bluestem (*A. scoparius*), 2.7 tons; and blue grama (*Bouteloua gracilis*), only 1.6 tons. Nearly half of this root material is in the top 4 in. of soil, and 70 to 80 per cent is in the top 12 in.

Rate and Periodicity of Growth

Because of the difficulties involved in studying roots, much less is known about their growth behavior than has been learned about shoot growth. Roots of some herbaceous species elongate rather rapidly. A rate of 0.5 in. per day is common in grasses, and wheat was observed to main-

tain this rate for over 70 days (Weaver, Kramer, and Reed, 1924). The principal vertical roots of corn have been observed to grow downward at the rate of 2 to 2.5 in. per day for 3 or 4 weeks (Weaver, 1925). Reed (1939) observed that the roots of young loblolly and shortleaf pine trees growing under field conditions elongated at a rate of nearly 0.1 in. per day during the period of maximum growth. Roots of loblolly pine made considerably more growth in a season than did those of shortleaf pine. Barney (1947) measured root elongation of loblolly-pine seedlings under controlled conditions in the greenhouse and observed that the maximum rate of growth was 3.4 to 5.2 mm. per day at the optimum temperature of 20 to 25°C. Holch (1931) reported that bur oak roots penetrated to a depth of 60 in. in prairie soil during the first growing season, but that red oak roots penetrated only 28 in. under the same conditions, illustrating differences in rates of growth for different species.

There has been considerable discussion as to the length of the growing season of roots, particularly those of woody plants. Some evidence of periodicity has been found, and several investigators have reported two principal periods of growth—one in the spring and the other in the autumn. Woodroof and Woodroof (1934) reported as many as four to eight cycles of root growth in pecan roots, in Georgia. According to Reed and MacDougal (1937), roots of citrus trees in California had two periods of growth—one from late March to late June, another in July and August. While rising temperature was doubtless responsible for the resumption of growth in March, these investigators did not believe that the cessation and resumption of growth during the summer could be attributed to environmental factors. Reed (1939) found that roots of loblolly pine (*Pinus taeda*) and of shortleaf pine (*P. echinata*) elongated during every month of the year but that they made the most growth in April and May and the least during January and February. The periods of slowest root growth in the winter coincided

with the periods of lowest soil temperature, while the periods of slowest root growth in the summer coincided with the periods of lowest soil moisture (see Fig. 21). Turner (1936) observed that root growth of loblolly and shortleaf pine in Arkansas occurred during every 8-day period for 2 years. The least elongation occurred in the winter, the most in the spring and again in early autumn or midautumn, with less growth during dry periods in the summer. Harris (1926) reported that in Oregon and British Columbia apple and filbert roots grow all through the year if they are not subjected to freezing, drought, or immersion in water. These studies were made in mild climates, where the soil seldom freezes below the surface. Stevens (1931) found that in New England no growth of white pine roots out of doors occurred from Nov. 15 to the first of April, but that roots of trees kept in the greenhouse grew as rapidly in the winter as in the summer. The author has observed that when dormant potted tree seedlings are brought into the greenhouse in the winter, root elongation often begins within a few days. Apparently roots, unlike the stems of many plants, have no inherent dormant period. It seems doubtful whether there is any inherent periodicity in root elongation. It is more likely that the periodicity observed is the result of variations in soil temperature, soil moisture, oxygen supply, or supply of food, though this view has been questioned by Reed and MacDougal, and by others.

There is, likewise, little evidence for any inherent periodicity in the growth of the roots of herbaceous plants, the observed examples of periodicity being attributable to variation in the environment. White (1937) found a seasonal periodicity in the growth of excised tomato roots cultured in flasks of nutrient solution, their growth being slower in the winter than in the summer. After some investigation, however, he attributed this difference to seasonal variations of temperature in the room where the cultures were kept. These root cultures were found to be unaffected by variations in light intensity. Raines and Travis (1937) reported

that seedling roots of several species that were germinated at constant temperatures in a laboratory grew more slowly in December than in October or May. Since temperature was constant and the seedlings were kept in darkness, neither light nor temperature could have been responsible for the differences. It was attributed to the lack of ventilation in the laboratory in the winter, with a resulting accumulation of volatile toxic substances of some sort.

Longevity of Roots

It has been generally assumed that the roots of most herbaceous plants are not very long lived. It is often stated that the primary, or seminal, roots of grasses, for example, live only a few weeks after germination and that the only permanent roots are the secondary roots, which arise adventitiously. This is by no means always true. It has been found that under certain conditions the primary roots of wheat, barley, rye, and various wild grasses are the only roots present and that they are capable of maintaining normal growth for an entire season. Weaver and Zink (1945) observed that at least part of the seminal roots of 14 species of grasses were alive and capable of absorbing after 3.5 to 4 months of growth. Later, Weaver and Zink (1946a) banded large numbers of roots of 10 species of prairie grasses with rings of soft tin and, although considerable differences existed between species, most of the roots survived one or two seasons and some were alive after three seasons. Stuckey (1941) observed that some species of grasses produce a new root system each year, while the root systems of other species are perennial and few new roots are added the second year.

It is assumed generally that the roots of woody plants are perennial. This undoubtedly is true of the larger roots. The primary root, for example, often develops into a tap root and attains great size and age. Even casual examination by means of trenching shows, however, that many of the smaller roots die every year and, according to Hatch, short

roots of pine normally live but one year. Probably most of this loss occurs during periods when the soil is too wet for good aeration and, unless these roots are rapidly replaced, tree growth may be seriously handicapped by lack of sufficient absorbing roots. It is well known that many of the fine absorbing roots of fruit trees die during the winter or after the soil has become saturated by irrigation or by heavy rains. This probably is true also of forest trees. Childers and White (1942) found the average life of small branches on apple roots to be only a week, even though environmental conditions seemed favorable to growth. Kinman (1932) reported the presence of numerous very fine lateral roots on fruit trees that died in a few days when the roots from which they were growing began to become suberized.

CHAPTER 6

FACTORS AFFECTING THE DEVELOPMENT OF ROOT SYSTEMS

The manner in which a root system develops depends both on its hereditary potentialities and on such environmental factors as soil texture, structure, moisture content, aeration, and temperature; kind and concentration of solutes; and competition with other roots. These factors will therefore be treated in some detail.

Heredity and Initial Root Habit

The type of growth of the root systems of seedlings of many species is firmly fixed by their heredity. This has an important bearing on their ability to absorb water and hence to survive droughts. Toumey (1929) concluded from extensive studies that most tree seedlings can be classified in one or two general groups—those with tap roots which grow rapidly downward and penetrate deeply and those with slowly growing, shallow primary roots and extensive, rapidly growing lateral roots. Bald cypress (*Taxodium distichum*) and yellow birch (*Betula lutea*) can become established only in wet areas, because their shallow seedling root systems do not enable them to survive where the soil dries out during the first year or two after germination. Upland hickories, red cedar (*Juniperus virginiana*), and many other upland species produce rapidly growing, deeply penetrating tap roots, which enable them to obtain water even after the surface soil has dried out during summer droughts. Red maple (*Acer rubrum*) has a root system which is readily modified by the environment. It develops numerous shal-

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low laterals in swamps and a deep tap-root system in dry upland soils, hence it is able to thrive on both dry and wet sites.
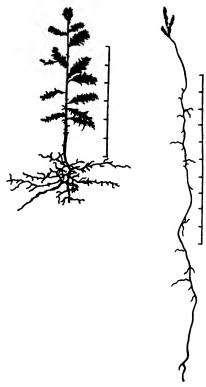
FIG. 18. Hereditary differences in root systems grown under similar environmental conditions. On the left is bald cypress (*Taxodium distichum*), which always produces a shallow, spreading root system. On the right is red cedar (*Juniperus virginiana*), which always produces a deep tap root. (*After Toumey, 1929.*)

Holch (1931) also found each of the several species of tree seedlings which he studied to have its characteristic root system. The roots of bur oak (*Quercus macrocarpa*), which occurs normally on dry ridges, reached a depth of 5.7 ft. the first season, while those of linden (*Tilia americana*), which usually grows on moist sites, penetrated only 1.2 ft. but spread out laterally. When grown under unfavor-

able conditions, as in the shade, root systems tend to be miniature replicas of those produced under favorable conditions.   Because of the shallow root system, the majority
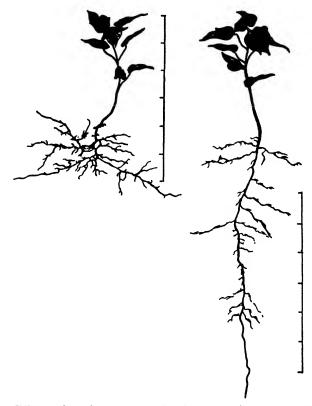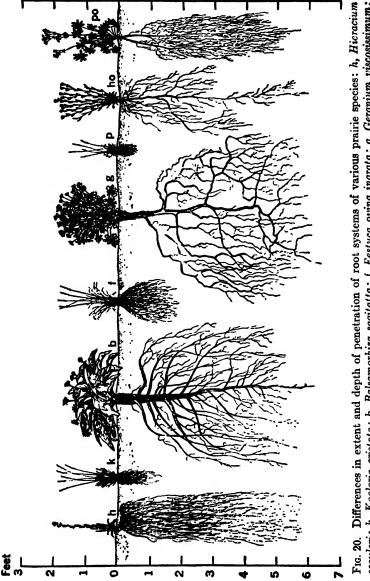
Fɪɢ. 19.   Effects of environment on development of root systems of red maple (*Acer rubrum*) seedlings. On the left is a typical seedling from a swamp, with shallow, wide-spreading roots. On the right is a seedling from a dry upland, with a deep tap root and weak laterals. (*After Toumey, 1929.*)

of the seedlings of linden died during the first summer in the comparatively dry soil of the open prairie.   Albertson and Weaver (1945) studied the survival of trees in the Prairie region after the great drought of the 1930's.   They concluded that root habit is one of the most important factors determining the drought resistance of trees, deep-rooted

species surviving much better than shallow-rooted species. Coile (1940) concluded that the deep tap roots of oak and hickory seedlings, which extend below the horizon of most intense root competition, enable them to survive droughts much better than do the more shallow-rooted pine seedlings. It has been found also that shallow-rooted seedlings, such as western hemlock (*Tsuga heterophylla*) and western cedar (*Thuja plicata*), suffer much greater mortality during droughts than do seedlings of such deep-rooted species as western white pine (*Pinus monticola*), western larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga taxifolia*), and lowland fir (*Abies grandis*) (Haig, 1936). Eastern hemlock and red cedar both germinate freely on open sites in southern New England during moist springs, but hemlock seedlings have shallow roots and die from desiccation as the surface soil dries, while the deep-rooted seedlings of red cedar survive and become permanently established (Toumey, 1929).

As seedlings grow older, the form of the root system often tends to be increasingly modified by environmental factors. A few species, however, possess root systems the forms of which are so firmly fixed by heredity that they are maintained, regardless of the environment. *Pinus contorta* typically develops a much more shallow root system than does *P. ponderosa;* hence it is restricted to moister sites than are required by the latter (Gail and Long, 1935). Hereditary differences in depth and form of root system are very noticeable in grasslands on which a number of species grow side by side. According to Weaver and Clements (1938), out of 43 species representative of the true prairie flora of eastern Kansas, Nebraska, and Iowa, 14 per cent have their roots restricted to the surface 2 ft., 21 per cent have roots extending below 2 ft. but seldom below 5 ft., and 65 per cent have roots extending deeper than 5 ft. Conspicuous differences exist, besides, in the extent and form of root systems of crop plants as revealed by the studies of Weaver and his associates. Representative of two very different

FIG. 20. Differences in extent and depth of penetration of root systems of various prairie species: *h, Hieracium scouleri; k, Koeleria cristata; b, Balsamorhiza sagittata; f, Festuca ovina ingrata; g, Geranium viscosissimum; p, Poa sandbergii; ho, Hoorebekia racemosa; po, Potentilla blaschkeana.* (*From Weaver, 1919.*)

types are horse-radish (*Amoracia rusticana*) and squash (*Cucurbita maxima*). A 10-year-old plant of horse-radish had a root system only 3 ft. in diameter, but it extended into the soil to a depth of 14 ft. A Hubbard squash plant 11 weeks old had a few sparsely branched roots extending to a depth of 6 to 7 ft., but most of its roots were in the surface 12 in. of soil, where they completely occupied a circle with a radius of 15 ft. (Weaver and Bruner, 1927).

Environmental Factors

While the hereditary potentialities are an important factor in the development of the root system, the environment is equally important. Included in the environment are soil characteristics, such as texture, structure, and depth; the amount of available water; the kind and concentration of salts; pH; aeration; and competition with the roots of other plants. Factors affecting the tops, such as grazing, cutting, defoliation by disease or insects, and shading, will also affect root development through their effects upon processes carried on in the tops. Although it is seldom practical to modify the aerial environment of a plant, the environment of the root can be modified by cultivation, fertilization, irrigation, and drainage.

Root Competition and Interaction. It has frequently been observed that when plants are grown close together their individual root systems are less extensive than when they are grown farther apart. Pavlychenko (1937a) reported that barley and wheat root systems were nearly 100 times larger when grown without competition than when grown in drill rows 6 in. apart, and that the presence of weeds further reduced the size of the root systems. Weaver and Kramer (1932) found that competition with prairie grasses greatly reduced the size of root systems of tree seedlings, and Yocum (1937) observed that growing corn between rows of young apple trees reduced extension of the apple roots both vertically and laterally. Coile (1940) attributed the smaller size of root systems of loblolly-pine

seedlings grown in a forest, as compared with those grown in the open, to the more intense root competition in the forest. The number of small roots and, hence, the intensity of root competition in the A horizon under a pine stand increase rapidly with the age of the stand, up to between 20 and 30 years, and then slow down. Coile suggested that after a forest stand reaches a certain age the number of small roots in the surface soil no longer increases. After the saturation point for roots is reached in a forest, it is very difficult for seedlings to become established.

Besides the obvious forms of competition for water and minerals, there is another phase of root interaction that often is important. It has long been observed that the growth of certain species seems to hinder the growth of subsequent crops through the effect of some factors left in the soil. Thus sesame and sorghum are claimed to reduce yields of succeeding crops, and walnut inhibits the growth of surrounding plants. At one time these effects were attributed to specific toxic substances excreted by the roots, but this view has been partially abandoned. Now it is believed that, in many instances, such injury is the result of depletion of nitrogen or of water by the preceding crop, the immobilization of nitrogen by microorganisms during decay of large amounts of organic matter, or the production of toxic substances during decomposition of roots and tops. Myers and Hallsted (1942) found at Hays, Kansas, where soil moisture is often limiting, that the lower the yield of the preceding crop, the greater was the yield of winter wheat in the succeeding crop. They believed that this was because good crops leave less water for the succeeding crop than do poor crops. Thus the yield of winter wheat after sorghum was less than that after corn because sorghum lowers the soil moisture more than corn does. Some instances of injurious effects of grass on tree growth are attributed to depletion of nitrates or of oxygen, or to production of excessive amounts of carbon dioxide in the soil by respiration of the grass roots (Howard, 1925). It has been suggested that one reason why

tree seedlings do not thrive in the dense sod of the prairie is because decomposition of organic matter and respiration of the grass roots produce a concentration of carbon dioxide too high for satisfactory growth of tree roots (McComb and Loomis, 1944).

By no means are all interactions between root systems deleterious. As roots become senescent, die, and decay, some mineral elements are released, which are absorbed by growing roots in the immediate vicinity. Much more important is the supply of available nitrogen provided by nitrogen-fixing bacteria on the roots of legumes. This was formerly believed to become available to other plants only after the death and decay of the legume roots, but Virtanen (1947) presents evidence that large quantities of nitrogenous compounds are secreted into the soil and then are absorbed directly by other plants. For example, when a heavy planting of oats was grown with peas, the oats absorbed so much of the nitrogen excreted into the substrate that the peas suffered. It has been reported frequently that the planting of legumes with nonleguminous species is directly beneficial to the latter. This is now believed to be the result of direct transfer of nitrogen through the soil.

In recent years, interest in the possible importance of plant secretions of various sorts has been renewed. According to Lucas (1947), there is evidence that certain algae excrete into the water substances which exclude certain animals from association with them. Templeman and Sexton (1946) observed that low concentrations of certain chemicals prevented germination or inhibited growth of various weeds but did not affect cereals. These observations led to the suggestion that the composition of terrestrial plant communities may be influenced by substances occurring naturally as the products of the dominant species of a given community. It may prove that, while certain species are more or less interdependent, others are excluded by root secretions. Bonner (1946) found that transcinnamic acid released into the surrounding medium by guayule roots in-

hibits growth of guayule seedlings. The next few years may witness interesting developments in this field. The older work is discussed in a review by Loehwing (1937) and in Miller (1938, pages 164–174).

Soil Moisture. Soil moisture affects root growth not only directly, but also indirectly, because it affects soil aeration. Holch (1931) and Duncan (1941) concluded that root growth of tree seedlings is inversely proportional to the available moisture content of the soil, and this probably is true of many species that have high oxygen requirements, provided that the moisture content does not drop to or below the permanent-wilting percentage. Since the effects of excessive soil moisture will be considered under aeration, this discussion will be concerned chiefly with the effects of deficiency of soil moisture. Cannon (1911) stated that the depth of penetration of root systems of plants in the Arizona desert depends on the depth to which the soil is wetted by rain. Weaver (1920) and Weaver and Crist (1922) found a similar relation, root penetration being greatest in well-watered prairie, less in mixed prairie, and least in the short-grass plains, which have so little rainfall that the soil is seldom wetted deeper than 1.5 to 4.0 ft. In the Plains area, where only the surface soil is wetted, roots do not penetrate below the hardpan which marks the lower limit of moist soil, except when periods of unusually heavy rainfall wet the soil to greater depths.

Differences of opinion exist concerning the ability of roots to grow into dry soil. Shantz (1927) wrote that certain trees of the African grasslands possess roots capable of extending into dry soil, but that ordinary crop plants cannot do so. Breazeale and Crider (1934) found that roots of at least certain species would penetrate into soil below the permanent-wilting percentage. They believed that water is absorbed from moist soil and translocated to roots in dry soil, where it diffuses out and wets the dry soil. They suggested that shallow-rooted plants may at times be dependent on water transported to the surface by plants that are

more deeply rooted. Hagan (1948) grew two sunflowers in the same container, so that their root systems were intertwined. When one plant was detopped and water was supplied to the root system through the stump, insufficient water escaped into the soil to maintain the turgidity of the intact plant, even when its top was enclosed in a moist chamber. From this Hagan tentatively concluded that very little water is lost from living roots to the soil at the permanent-wilting percentage.

It is doubtless true that where roots are in contact with dry soil some loss of water might occur, but it is unlikely that the moisture content of the dry soil would be raised above the permanent-wilting percentage, because equilibrium between root and soil with respect to water movement probably is attained at or slightly below the permanent-wilting percentage. Furthermore, most roots in dry soil cease to elongate and become suberized up to the tip—a condition that presumably decreases water loss. Guayule is a native of arid regions, but Muller (1946) reported that its roots do not penetrate dry soil and that, as the soil in the root zone dries out, growth ceases and the roots become suberized. Hendrickson and Veihmeyer (1931) found that when root systems developed in moist soil, separated from dry soil by paraffin partitions, the root tips penetrated through the partitions but grew only a few millimeters into the dry soil. Hunter and Kelley (1946b) grew corn plants in containers having walls of cheesecloth waterproofed with paraffin, plus road oil. Roots grew through the walls into the surrounding dry soil and increased the moisture content measurably, although not as high as the permanent-wilting percentage. Radioactive phosphorus had been incorporated with the dry soil, but there was no evidence that this element was absorbed. Volk (1947) also reported that corn roots grew into sand and silt loam soil with a moisture content below the permanent-wilting percentage and increased the moisture content of the dry soil. Nitrogen and potassium were absorbed from the dry soil, but not phosphorus.

He concluded that single roots cannot penetrate dry soil, but that only large masses of roots growing together can penetrate it.   Root growth of loblolly and shortleaf pine slows
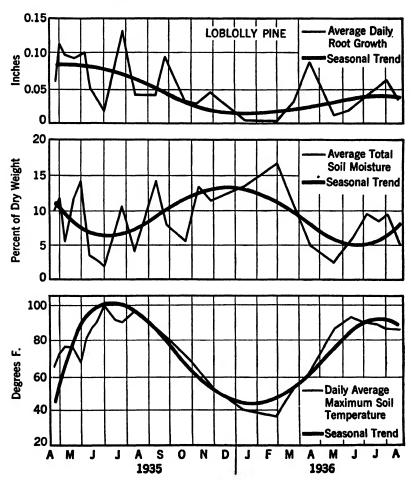
Fɪɢ. 21.   Effects of soil moisture and soil temperature on elongation of loblolly pine roots.   (*From Reed, 1939.*)

down as the soil approaches the permanent-wilting percentage (Reed, 1939), and the same is said to be true of jack pine (Kaufman, 1945).   It seems unlikely that under field conditions any significant amount of root growth occurs in soil at or below the permanent-wilting percentage.

In general, larger root systems are produced in soil that contains an abundance of soil moisture if aeration is good, but a larger ratio of roots to shoots is obtained when there is a limited supply of water. Relatively large root systems, compared to tops, are highly desirable for planting stock of both herbaceous and woody species. Avoidance of over-watering is one thing which will help to produce a type of plant desirable for transplanting.

It has long been assumed that roots grow toward moist soil, or show hydrotropism. Recent research indicates that not all roots show hydrotropism, and that probably it is actually rare under field conditions (Loomis and Ewan, 1936). Certainly it is much weaker than geotropism, for the roots of many species will grow downward out of moist soil into dry soil until elongation is stopped by desiccation, instead of turning at an angle and staying in the moist soil. The average layman has a strong belief that roots can some-how detect water at a distance and grow toward it. This is based on the observation that large masses of roots develop in leaky drainpipes and other well-watered areas where the aeration also is good. Oppenheimer (1941), who described large masses of roots formed under dripping water taps, suggested that aeration was as important as moisture in governing their formation. It is not generally realized that roots are continually growing outward in all directions from plants. Roots of trees, for example, often extend to a distance two or three times greater than the radius of the crown. Whenever these roots, extending at random, reach an area where there is an abundance of moisture as well as good aeration, they branch profusely and develop large masses, but there is no evidence that they actually grow toward moist soil from dry soil.

Soil Aeration. Everyone is familiar with the yellowing of leaves, reduction in growth, and eventual death of crop plants when the soil in which they are growing is saturated with water. This occurs because of injury to or death of the root systems. That this injury or death is caused by

lack of oxygen and possibly by accumulation of carbon dioxide, rather than by the direct effects of water, is indicated by the fact that most species of plants make satisfactory growth in well-aerated water cultures. Arnon and Hoagland (1940) found the average dry weight of roots per plant of tomato grown in aerated water culture to be 19.9 gm., and the weight of roots on plants grown in unaerated cultures to be only 12.4 gm.

Respiration of soil organisms and of roots continually depletes the oxygen and adds to the carbon dioxide content of the soil atmosphere and of the water films in equilibrium with it. The activity of soil organisms varies with temperature, moisture, and the supply of organic matter that they can use as food. By the addition of starch and ammonium sulfate to soil, such an increase in soil organisms was produced that all free oxygen disappeared and wheat seedlings growing in the soil died (Karsten, 1939). It has been suggested that decomposition of organic matter, plus respiration of grass roots, produces in prairie soils oxygen and carbon dioxide concentrations that are unfavorable for the growth of tree roots, and that this may be one of the factors tending to prevent invasion of the grasslands by forest. In India, several species of trees were found to be quickly injured or killed by development of a heavy sod over their root systems, and it was concluded that at least part of this injury resulted from an excess of carbon dioxide produced by the grass roots (Howard, 1925). Romell (1932) calcu-lated that the combined activity of roots and of soil organisms produces from 0.2 to 0.4 gm. of carbon dioxide per square meter of soil surface per hour in forest soils.

Most of the exchange of gases between the soil and the atmosphere is accomplished by diffusion, though some movement may occur because of pressure gradients produced by temperature differences, changes in barometric pressure, wind, and the downward percolation of gravitational water. Adequacy of soil aeration depends largely upon soil texture and structure, because gas exchange occurs through the

larger or noncapillary pores, which are free of water at mois-
ture contents lower than field capacity. Aeration is there-
fore almost never limiting in sandy soils but is often quite
inadequate in fine-textured soils, particularly if they are
poorly granulated. Soils having less than 10 or 12 per cent
of their volume as pore space free of water when the soil is
at field capacity are likely to be poorly aerated. Leonard
(1945) found the oxygen concentration under cotton to vary
from 0 to 21 per cent in clay, from 10 to 21 per cent in a
fine sandy loam, and from 18 to 21 per cent in sandy loam.
As the soils dried out during the summer, the oxygen con-
tent increased, particularly in the clay that cracked as it
dried; but early in the summer the oxygen content was often
limiting in the clay, though not in the coarser textured soils.
Salter (1940) calculated that if the upper 2 in. of the soil
are puddled or compacted, as by trampling when wet, so
that the capillary pore space is reduced from 25 to 5 per
cent, the concentration of carbon dioxide below the com-
pacted layer in an average forest soil will be four times as
great as it would be in the absence of such an impermeable
layer.

Obviously, an impermeable layer near the surface is more
serious than one deep in the soil, because most of the roots
and the biological activity are near the surface. Huberty
and Pillsbury (1943) found in avocado orchards well-
defined horizons of very impermeable soil, which hindered
drainage and gas exchange, with resulting injury to the root
systems and with consequent decline of the trees. Girton
(1927) emphasized the importance of plow sole, hardpan,
and other impermeable layers which hinder aeration in cit-
rus orchards. Decline of citrus fruits often follows injuries
to root systems that result from poor aeration in water-
logged soil, and much damage to citrus has occurred be-
cause of excessive irrigation. According to recent investi-
gators, the most important factor in preventing slow de-
cline of citrus trees is to avoid overwatering and long-con-
tinued saturation of the soil (Klotz, 1945).

It is generally agreed that the poorer drainage and aeration of the finer textured Eastern soils are largely responsible for the fact that root systems seldom penetrate so deeply in the East as in the Prairie region and other areas where the texture of the soil is coarser. This difference in root penetration is illustrated by the difference in behavior between corn on a well-aerated soil in Illinois and that on a poorly aerated soil in the Piedmont of North Carolina. Reimann, Van Doren, and Stauffer (1946) found that corn flourished on a very permeable silt loam soil in Illinois, although by early August no available water remained in the upper 3.5 ft. and absorption was occurring from as deep as 5 or 6 ft. In contrast, James (1945) found that corn on a heavy-phase Cecil clay loam in North Carolina was so shallow-rooted that it was unable to absorb sufficient water from a depth of 3.5 ft., to prevent death from desiccation. Coile (1948) found the growth of pine in the Piedmont closely related to such physical properties of the soil as its plasticity and the amount of swelling when wetted. Where the B horizon exhibits marked swelling when wet, the internal drainage is poor, the soil becomes waterlogged during wet periods, and the root systems suffer from inadequate aeration. This decreases top growth. Coile concluded that space for roots to grow and physical characteristics that control moisture availability and aeration are the primary factors determining the quality of land for forests.

Boynton (1941) and others working in New York orchards have found poor drainage and inadequate aeration to be frequently limiting factors in appletree growth. Heinicke (1932) observed that flooding the soil containing apple roots during the winter caused considerable loss of small roots but produced no serious injury if the soil was drained before leaves began to appear. Flooding in the summer soon caused injury, particularly if transpiration was rapid. Boynton agreed with earlier investigators that the oxygen concentration of soil atmosphere decreases and that carbon dioxide concentration increases with (1) increased depth,

(2) increased temperature, and (3) decreased air space in the soil pores. The carbon dioxide concentration rarely rose above 12 per cent and usually was much lower, but Heinicke and Boynton (1941) observed a concentration of 33.6 per cent in one sample and an average of 12 per cent on a plot of heavy soil during the growing season. The oxygen concentration generally varies over a wider range than does the carbon dioxide concentration; and while the sum of the oxygen and carbon dioxide concentrations usually approximates 20.8 per cent, it sometimes deviates widely from this value. Since the soil at Ithaca, New York, is usually saturated during the winter and dries out during the summer, the oxygen concentration is lowest in the spring and rises during the summer. The carbon dioxide concentration also increases during the summer, presumably because of increased biological activity with increasing soil temperature (Boynton and Compton, 1944).

In soil that is quite impermeable to gases, the concentration of carbon dioxide might be much higher, and the concentration of oxygen much lower, near a root or a group of rootlets than a short distance away. Analyses of total soil atmosphere may, therefore, sometimes fail to reveal the actual condition in the immediate vicinity of the roots.

There has been some debate concerning the relative importance of low oxygen and high carbon dioxide on root growth. Lundegardh (1931, page 263) states that roots of wheat and some other species are very sensitive to as little as 1 per cent of carbon dioxide, but results of more recent work do not indicate that roots are very sensitive to carbon dioxide at the concentrations usually found in the soil. Leonard (1945) and Leonard and Pinckard (1946) found that the root growth of cotton was not inhibited in solution cultures saturated with gas mixtures containing up to 15 per cent of carbon dioxide, was slightly inhibited by 30 per cent, and ceased at 60 per cent. The oxygen concentration in these experiments was kept at 21 per cent. Whitney (1942) found that 20 per cent of carbon dioxide plus 20

per cent of oxygen did not injure the roots of several herbaceous species, but in the absence of oxygen it did injure coleus and tomato roots. Erickson (1946), noting that tomato roots are uninjured by as much as 6.8 per cent carbon dioxide, concluded that roots in unaerated cultures are injured by lack of oxygen, before excess of carbon dioxide has become limiting. It appears probable that the concentration of carbon dioxide in the soil is seldom high enough to be very toxic to the roots of most plants, but the concentration of oxygen is often too low for best root growth. The effects of carbon dioxide on the absorption of water and of salt are discussed in Chaps. 9 and 10.

The oxygen requirements for root growth have been investigated by numerous workers. According to Cannon (1925), roots of many species will make slight growth at 0.5 to 2.0 per cent, but 8 to 10 per cent is usually necessary for good growth. He also found that for good growth a higher oxygen concentration is required at high than at low temperatures. It is probable that good aeration generally is more important at high than at low temperatures. Girton (1927) found that orange root growth was stopped with 1.2 to 1.5 per cent of oxygen and retarded with 5 to 8 per cent, at 28°C. Boynton, DeVilliers, and Reuther (1938) observed that apple roots can exist in soil atmospheres containing 0.1 to 3.0 per cent of oxygen and can grow slowly with 3 to 5 per cent, but that more than 10 per cent is necessary for good root and top growth. Later, Boynton and Compton (1943) found that apple, peach, and prune trees growing in tanks of nutrient solution showed reduction in root and shoot growth when the tanks were aerated with nitrogen containing less than 20 per cent of oxygen. There is said to be a relatively short period of time in most New York orchards when enough oxygen for good root growth occurs in clay soils at depths greater than 3 ft. Leonard and Pinckard (1946) found that cotton roots thrive in solutions aerated with 7.5 per cent or more of oxygen. The minimum concentration necessary for measurable elonga-

tion was between 0.5 and 1.0 per cent at 28°C., and 90 to 100 per cent oxygen also retarded root growth.

It is interesting to find that too much oxygen is toxic to roots. Loehwing (1934) reported that, while aeration of sand and soil in which beans and sunflowers were grown resulted in larger roots and shoots and larger root-shoot ratios, excessive aeration decreased the size of the plants. It is generally agreed that different species have different oxygen requirements. The optimum for soybeans is lower than the concentration in equilibrium with the normal atmosphere at ordinary growing temperatures, and a higher concentration is toxic. Growth of tomato and oats increased with increased oxygen concentration to the highest concentration used, which was more than twice that of the atmosphere (Gilbert and Shive, 1942). These results indicate that the oxygen concentration occurring naturally in well-aerated, fertile soil is not high enough for the best growth of some plants, such as tomato, though it is adequate for others, such as certain cereals (Arnon and Hoagland, 1940).

Durell (1941) grew tomato plants in shallow tanks containing nutrient solution with various degrees of aeration; also in a tank filled with sandy loam soil. Vegetative growth and yield of fruit were greater, even in slightly aerated solution cultures, than they were in soil; this indicates that aeration can be limiting to growth even in a shallow tank of well-drained soil. Slight aeration sufficed for optimum growth of roots and yield of fruits, but the greatest dry weight of stems and leaves was obtained at the highest rate of aeration. Apparently the aeration requirement for optimum root and fruit development is much lower than for optimum shoot growth. Durell did not discuss this situation, but possibly shoot growth is stimulated by higher rates of aeration because of increased absorption of mineral nutrients in better aerated solutions.

An excellent example of the differences between species is afforded by experiments of Vlamis and Davis (1944) on rice,

barley, and tomato. Aeration of cultures with ordinary air increased root and shoot growth of tomato 100 per cent, caused a small increase in barley, and had no effect on the size of the root systems of rice, though some injury to root tips occurred in aerated cultures. Submergence in water of root systems growing in soil killed tomato and retarded barley, but greatly increased root growth of rice. Saturating solution cultures with carbon dioxide reduced the root growth of rice as much as it did that of barley and tomato; but saturation with methane increased rice root growth, though growth of barley and tomato was reduced. Excised roots of rice are just as sensitive to low oxygen concentrations as are those of barley and tomato, but the roots of entire rice plants are much less affected than are the roots of entire barley and tomato plants. This suggests that rice roots are supplied with some oxygen from the shoots. There is considerable other evidence that oxygen can diffuse down through the stem from the leaves to submerged roots and rhizomes of some species through the aerenchyma charactristic of hydrophytes (Conway, 1940; Glasstone, 1942; Laing, 1940*b*). It appears probable that part of this oxygen is a by-product of photosynthesis in the shoots, since the concentration in the roots seems to increase when the tops are exposed to light (Cannon, 1932; Laing, 1940*b*).

It is likely that the roots of many species characteristic of bogs and swamps are able to carry on anaerobic respiration without injury (Laing, 1940*a*). Weaver and Himmel (1930) reported that certain swamp species developed just as large root systems in continuously saturated soil as they did in soil alternately saturated and drained, and that they were larger than those developed in well-aerated soil. Although cranberries are native to bogs, they sometimes are injured by lack of oxygen (Franklin, Bergman, and Stevens, 1943). Caughey (1945) found that roots of certain bog shrubs are injured as readily by poor aeration as are those native to well-drained sites. Bog plants are usually shallow rooted and some are so located on hummocks that their

roots are fairly well aerated during most of the growing season, even though they are largely submerged during the winter and early spring. McQuilkin (1935) found roots of *Pinus rigida* extending several feet into saturated, sandy soil and branching extensively. Mycorhizae occurred on many of the smaller roots. In these pine roots, no large air spaces or other anatomical variations of the type often found in submerged roots occurred. It is interesting to find a species which thrives on xeric sites that is able to grow in saturated soil, as well.

It is said that in saturated soils containing organic matter toxic concentrations of ferrous iron, sulfides, and manganese are commonly developed because the carbon dioxide produced by biological activity enables abnormally high concentrations of these substances to exist in solution (Robinson, 1930). Thus other factors besides aeration may limit root growth in saturated soil.

As is obvious, poor soil aeration resulting from excessive moisture content can be greatly improved by adequate drainage. In very heavy soils, even adequate drainage is not sufficient to ensure good growth of apple trees, and they ought not be planted on such soil. Heinicke and Boynton (1941) found that a special aeration system was necessary to obtain good growth of apple trees on certain plots where they had never previously thrived. These investigators installed tile drains every 6 ft., in trenches 4 ft. deep, the lower 2 ft. of which were filled with gravel with earth on top, the entire system ending in a shallow well. They also found that decline of mature apple trees could be stopped by providing aeration close to the trunk, through tile covered with gravel.

It has been demonstrated that cultivation sometimes increases crop yields on soils having inadequate pore space, because it improves aeration. On soils that have good structure and adequate pore space, cultivation in itself, independently of weed control, often has little or no beneficial effect on crop yield. Unfortunately, cultivation not only

damages shallow roots but also eventually causes deterioration of soil structure, particularly if the soil is cultivated when wet (Baver, 1948). It therefore is necessary to balance the advantages and the disadvantages of cultivation—beyond that necessary for weed control—according to local soil conditions.

Several interesting problems concerning the relation of aeration to root growth and absorption remain more or less unsolved. One problem is why we can grow most crop plants in solution cultures, often without any special aeration, although plants of the same species are severely injured or killed if the soil in which they are growing is flooded. The author has observed that when seedlings are transferred from soil to water culture the roots produced in the soil usually die and are replaced by new ones. Possibly cells and tissues produced in water have a lower oxygen requirement than do those produced in soil. This is suggested by the observation of Steward, Berry, and Broyer (1936), who stated that cells developed directly in water withstand a lower concentration of oxygen, without limiting respiration or salt accumulation, than will tissues developed in a well-aerated medium. Another possibility is the existence, in roots that are produced in unaerated media, of morphological modifications which facilitate movement of gases from shoots to roots. Although the mechanism involved is not understood, it is well known that tissues produced in poorly aerated media often contain large air passages. Bryant (1934), for example, observed that roots of barley grown in unaerated culture solution were about 15 per cent greater in diameter and contained much larger air spaces in their cortical tissues than barley roots grown in aerated solution. The large air spaces in the cortex might facilitate movement of oxygen to the roots from the shoots.

The exact cause of the death of plants in flooded soil is not thoroughly understood. Flooding is accompanied by a rapid drop in transpiration, followed in a few days by yellowing and death of the leaves in many species. Possibly

toxic substances escape from the roots into the shoots and cause closure of the stomates and, after a few days, the death of the leaves. Since water is absorbed freely through root systems killed by heat or ether, mere death of the roots should not at once reduce transpiration materially or cause immediate injury to the shoot. Possibly the water-conducting system is plugged by materials formed by the dying root cells. This problem deserves further investigation.

Temperature. The beginning and end of the seasonal cycle of root growth is controlled largely by temperature, except in the tropics. Freezing of the soil or even near-freezing temperatures usually stop root elongation, though growth sometimes continues in the deeper, unfrozen regions when it has ceased near the surface. Batjer, Magness, and Regeimbal (1939) found that, when the soil was cooled to 4.5 to 7°C., root growth of apple trees was practically stopped, shoot growth ceased, and nitrogen absorption occurred very slowly. Collison (1935) observed slow elongation of apple roots in unfrozen soil covered by 2 ft. of frozen soil. In mild climates, root growth often continues all winter at a reduced rate. Crider (1928) found that roots of Prunus, *Covillea tridentata, Simmondsia californicum, Cupressus arizonica,* and *Opuntia laevis* grew all winter in Arizona, while roots of *Citrus aurantiacum, Vitis vinifera, Prosopis velutina,* and *Parkinsonia torreyana* ceased growth from early December to late March. Woodroof and Woodroof (1934) found that pecan roots grew very slowly at 4 to 7°C. and growing root tips were killed at −2°C., but that in Georgia at the depth of 1 ft. soil temperatures were never low enough to prevent pecan root growth.

Roots of species native to warm climates cease growth at higher temperatures than do those of cool climates. The minimum temperature for elongation of roots of germinating cotton seed is 16 or 17°C., and the optimum is 33 to 36° during the first 4 or 5 days, then decreases to 27°C. (Arndt, 1945). The maximum temperature is 39°C., only slightly above the optimum, and injury soon occurs at this

temperature. Bermuda grass made no growth at 4.5°C. and little growth at 10°, and the rate increased with temperature up to at least 38°C. Kentucky and Canada bluegrass roots grew well at 4.5°C., and the optimum temperature was only 10° for Canada bluegrass and 15°C. for Kentucky bluegrass; both species were severely injured at temperatures favorable to Bermuda grass (Brown, 1939). Girton (1927) found that the minimum temperature for growth of roots of grapefruit, sweet orange, and sour orange, in solution culture, was 12°, the optimum was 26°, and the maximum was 37°C.

Barney (1947) found that roots of loblolly pine seedlings grew most rapidly at 20 to 25°C., and that the rate of elongation at 5° and at 35°C. was less than 10 per cent of the maximum rate. At 35° most of the roots appeared to be dormant. His results are given in Fig. 22. Sections showed no mitotic figures, the tissues were differentiated up to the embryonic region, and the entire root tips appeared to be inclosed in a layer of suberized cells. The ratio of tops to roots was much smaller at 20°C. than at higher and lower temperatures, most of the difference resulting from variation in the amount of root growth rather than from variation in shoot growth. Adams (1934) found that cooling the soil decreased root growth of white pine seedlings much more than it did shoot growth. In Minnesota, *Pinus banksiana* roots ceased growth in October and resumed it in April, when the soil warmed up to 4 or 5°C.; but growth was slow until the soil temperature exceeded 10°C. (Kaufman, 1945).

Evidently high soil temperatures may be as limiting to root growth as are low temperatures. The temperature of the surface of soil exposed to the sun is often high enough to injure roots and the bases of stems (Bates, 1924; Korstian and Fetherolf, 1921; Pearson, 1931; Shirley, 1936). Temperatures of 50 to 70°C. have been observed in the surface inch of soil, while Shirley found that the roots of several species of conifers are killed in a few hours at 46°C. Nightingale (1935) found optimum root growth of apple

and peach at 18°, some decrease even at 25°, and very little growth at 30 to 35°C. High temperatures hastened root differentiation, so that the absorbing surface was greatly reduced. It is claimed that the root surface of strawberries is reduced so much at high soil temperatures that absorption
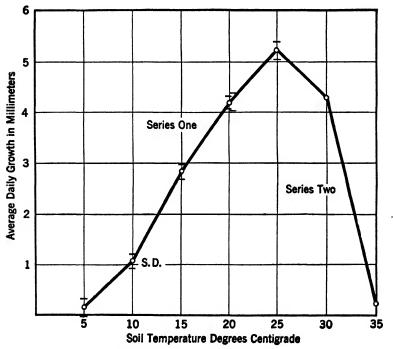
Fig. 22. The effect of soil temperature on the elongation of roots of loblolly pine seedlings. (*From Barney, 1947.*)

is hindered, with injury of the tops resulting from lack of water (Gray, 1941). The small number of roots occurring in the surface foot of soil in many California orchards is attributed by Proebsting (1943) to injuriously high soil temperatures of summer. Judging from the data of Smith (1929), summer soil temperatures at Davis, California, are often too high, near the surface, for good root growth.

It is interesting to note that while root growth of most species slowly increases with increasing temperature over a

range of 20 or 25° from minimum to optimum temperature, a further increase of only 5 to 10° above the optimum causes partial or complete cessation of growth of some species. This was observed in cotton by Arndt (1945), in loblolly pine by Barney, in tomato root systems by Riethman (1933), and in excised tomato roots by White (1937).

Much injury is caused to alfalfa, to cereals, and sometimes even to tree seedlings by frost heaving. Repeated freezing and thawing lifts the plants up, breaking off their roots below the surface, thus resulting in the death of the plants from desiccation. Mechanical strength of roots may, therefore, be an important factor in winter survival (Lamb, 1936).

Mineral Nutrition, Salt Concentration, and pH. It is well known that when roots penetrate into areas of the soil containing an abundance of minerals they branch profusely (Weaver and Clements, 1938). Anyone who has left a compost heap near a tree undisturbed for a few months has observed the extensive root development in the moist, fertile, well-aerated compost. The addition of commercial fertilizers to the upper few inches of soil undoubtedly favors the concentration of roots of crop plants near the surface. Not so much is known about the specific effects of various elements on roots as on shoots; but it is recognized that phosphorus stimulates root growth, and that deficiencies of boron and calcium produce short, stubby branches, while the root tips often die. In general, an abundance of the essential mineral elements—particularly nitrogen—stimulates root growth; but shoot growth is increased even more, so the ratio of shoots to roots is usually higher in fertile than in infertile soils. Bushnell (1941) found that potato roots are confined mostly to the upper 10 in. in silt-loam and sandy-loam soils, although they penetrate to a depth of 4 ft. in muck. Loosening the soil with a subsoiling tool caused little increase in depth of rooting, but addition of fertilizer to the subsoil caused deep rooting. He concluded that roots fail to penetrate deeply in these soils because of

lack of nitrogen and phosphorus. Farris (1934) concluded that in humid regions roots are limited largely to the surface soil by the high concentration of nutrients near the surface.

Soil acidity also affects root growth to a certain extent, though recent investigations indicate that good root and shoot growth of at least some species is possible over a wide pH range if precautions are taken to ensure an adequate supply of all essential mineral elements (Arnon and Johnson, 1942). Girton (1927) found best growth of roots of citrus fruits near neutrality and reduction of growth at pH 4 and pH 9. Guest and Chapman (1944) concluded that no direct injury occurs to roots of sweet-orange seedlings over a pH range from slightly below pH 4.0 to somewhat above pH 9.0, though indirect effects are observed at both extremes. According to Chapman (1941), shortleaf pine seedlings usually die at or soon after emergence in neutral or alkaline soils and in soils containing large amounts of soluble calcium, and thrive only in acid soils. In contrast, Howell (1932) concluded that, under field conditions, other factors have more influence than pH on the growth of ponderosa pine seedlings. Survival occurred from pH 2.7 to 11.0, but satisfactory growth occurred only from pH 3.0 to 6.0, probably because at higher pH values elements such as iron became unavailable. Probably much of the effect of soil pH on plant growth is indirect, either because the availability of certain elements is reduced or because solubility is increased to such an extent that toxic concentrations occur.

In arid regions, including most of the irrigated regions of the United States, salts often accumulate in the soil until the concentration is too high for satisfactory plant growth (Hayward and Magistad, 1946). The principal effects are produced through decreased availability of water; but specific salt effects also occur, because growth of some species is reduced more by chlorides than by sulfates, while the reverse is true of others. Root growth of peaches was reduced

more on Lovell than on Shalil rootstocks and reduced more by sulfates than by chlorides (Hayward, Long, and Uhvits, 1946). High concentrations of salts tend to cause slow root elongation and rapid maturation, with suberization occurring up to the tip, so that the roots resemble those in the dormant condition (Hayward and Blair, 1942). Still higher concentrations completely inhibit root growth, but considerable differences in salt tolerance exist between species. Wadleigh, Gauch, and Strong (1947) grew crop plants in soil containing various salt contents. Few bean roots penetrated into soil containing as much as 0.1 per cent of sodium chloride, and few corn roots penetrated soil containing 0.2 per cent; but a few alfalfa roots penetrated into soil containing 0.25 per cent sodium chloride, and cotton roots were abundant in this soil.

Root and Shoot Relations

It appears that the proportion of roots to shoots is determined by the heredity of the plant as well as by its environment. Thus, according to Roberts and Struckmeyer (1946), a given environmental factor does not have the same effect on the root-shoot relations of all species. For example, many species have more roots in proportion to shoots with low night temperatures or with short photoperiods, but the reverse is true of other species. Since roots are dependent on their shoots for the carbohydrates essential to growth, whatever affects photosynthesis and the use of carbohydrates in the shoot will also affect root growth. Reciprocally, any injury to or inadequacy of the root systems will hinder shoot growth. In general, root and shoot growth are rather closely correlated and, if the development of one is modified, growth of the other is likewise modified. Nevertheless, considerable variation in relative proportions of roots and shoots occurs and this can be controlled by varying the conditions under which the plants are grown. Heavy grazing or too-frequent cutting, it is well known, will reduce root growth and even cause death, either directly

or, as often happens, by winterkilling or by drought (Graber, 1931; Graber, *et al.,* 1927; McCarty, 1938). Parker and Sampson (1931) reported that a single clipping of grass caused a cessation of root growth for more than 10 days and clipping at 15-day intervals for 4 months resulted in a 90 per cent reduction in yield of tops and roots. Biswell and Weaver (1933) found that four to seven clippings of several species of grasses reduced dry weight of the roots to an average of 10 per cent of the unclipped controls. Robertson (1933) also reported.large reductions in size of root systems caused by clipping. Weaver and Darland (1947) found the number and rate of growth of new roots in the spring a valuable indicator of the vigor of range grasses. Frequently clipped or overgrazed plants develop very few new roots compared to unclipped and ungrazed plants, and many of the old roots die.

Reduction in photosynthetic surface resulting from injury to leaves by hail, insects, or fungi will also be reflected in reduced growth of the root system. Another example of the possibility of affecting root growth by treating the shoot is indicated by the report of Fults and Payne (1947) that spraying bean shoots with DDT increased the number of branch roots, while spraying with Colorado 9 decreased the number. If this proves to be true under field conditions, it suggests the possibility of increasing the absorbing surface of a root system. This would be particularly desirable during dry periods, when intake of water and possibly of minerals is limiting to growth.

Shading usually reduces both the absolute size of root systems and the ratio of roots to shoots. Biswell (1935) found the root systems of several species of deciduous tree seedlings to be larger in full sun than in half sun. According to Mitchell (1936) and Gast (1937), white pine seedlings have larger root systems and larger root-shoot ratios when grown in full sun than when grown with shade. This is true, however, only when all other conditions, such as soil moisture and minerals, are favorable. Root systems of

loblolly pine grown in the open are larger than those in the shade (Coile, 1940; Kozlowski, 1947). Bakke and Gaessler (1945) reported that roots of bindweed (*Convolvulus arvensis*) grown with but 600 foot-candles of light for 4 years weighed only 0.3 per cent as much as roots of plants grown in full sun. Hoagland (1944) found that the proportion of roots to shoots of barley seedlings grown in culture solutions is considerably higher in the summer than in the winter. The difference was attributed to the decreased illumination existing in the winter, which reduces the supply of carbohydrates available to the roots. Barney (1947) observed that low light intensity decreased or even stopped root elongation of loblolly pine seedlings (see Fig. 23). Miller (1943) observed that roots of *Juniperus virginiana* trees suppressed by shading are much more susceptible to attacks by *Fomes annosus* than are the roots of trees growing in the open. Possibly this is because root systems of shaded trees are growing less vigorously and therefore are more susceptible to attack.

It has long been known that the development of fruits and seeds usually modifies the course of vegetative growth (Murneek, 1925). Roberts and Struckmeyer (1946) state that plants consistently have fewer roots in proportion to shoots when flowering. An example of the extent to which root growth can be affected by fruiting is described by Eaton (1931). Cotton plants on which no bolls were allowed to develop had roots with a dry weight triple that of roots on control plants bearing bolls. The ratio of roots to shoots was approximately tripled by removal of both bolls and vegetative buds, with consequent prevention of both branching and boll formation. Later Eaton and Joham (1944) showed that boll formation is accompanied by reduced movement of sugar to the roots, which no doubt causes the reduced root growth. Nutman (1933) reported that a heavy crop of coffee often so depletes the carbohydrate reserves in roots of coffee trees that many roots die, and this causes serious injury to the trees.

Besides furnishing carbohydrates, the shoot apparently supplies the roots with hormones necessary for their growth. In addition to auxin, at least one other substance produced in the shoot—termed by Went (1938) rhizocaline—is necessary for root growth. It is well known that in apple the type of scion used can modify the development of the root
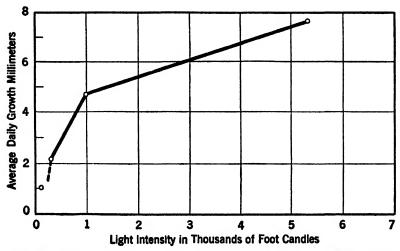
FIG. 23. Effect of light intensity to which the shoot was exposed on rate of elongation of roots of loblolly pine seedlings. (*From Barney, 1947.*)

system, possibly through the kind and quantity of hormones supplied to it. According to Went, the roots also produce a hormone, caulocaline, necessary for stem growth; inadequate production of this substance will hinder stem growth. He believes that dwarfing of the scions on certain rootstocks may be the result of failure of the rootstocks to produce enough caulocaline, rather than failure to develop an adequate absorbing surface. Went (1943) believes aeration is even more important for the production of caulocaline than for salt absorption and suggests that caulocaline is produced by the shallow, better aerated portion of the root system.

Evidently the physiological characteristics of root systems have important effects on the success of the tops. It

has been found that the amounts of various mineral elements in the leaves and the chemical composition of the fruits of certain citrus varieties are affected by the rootstocks on which they are grown (Haas, 1945, 1948; Sinclair and Bartholomew, 1944). The greater resistance of certain rootstocks to injury from fungi and from poor aeration makes them much more desirable than others, which are quite susceptible to injury. Decline of lemon has been found to be much more prevalent in trees on sour orange stock than in trees on sweet orange, and trees on Sampson tangelo rootstocks are unusually resistant to decline (Batchelor and Rounds, 1944; Klotz, 1945).

Certain physiological differences between roots and shoots appear to exist. Marsh and Goddard (1939) found respiration of roots and immature leaves of carrot to be inhibited by sodium azide, hydrocyanic acid, and carbon monoxide, but these substances did not inhibit the respiration of mature leaves. Merry and Goddard (1941) found that a similar situation exists in barley. This was interpreted as indicating that during maturation a change occurs in the respiratory enzyme system of leaves—cytochrome oxidase, which is an important enzyme in roots and young leaves, being absent from mature leaves. Dawson (1942) demonstrated that nicotine is synthesized in the roots but not in the tops of tobacco plants. Kelly and Somer (1948) reported that the ascorbic acid content of potato tubers is controlled by the genetic constitution of the root system and is independent of the type of top grafted on a particular root system.

Glasstone (1947) reported that the mineral nutrient requirements of roots cultured alone are quite different from those of entire plants. Excised tomato roots grew well in a nutrient solution containing sucrose, vitamins, and the usual salts, but no boron, manganese, or zinc except that occurring as impurities. Much higher concentrations of these elements are necessary for satisfactory growth of entire plants

than could have occurred as impurities in the solutions in which the root cultures throve.

Toxic Substances

The possibility of excretion of toxic substances from roots has already been mentioned under the subject of root interactions. Apparently the toxicity once attributed to root excretions is largely the product of decomposition of roots and other organic matter in the soil. Benedict (1941), for example, attributes the tendency of thick stands of *Bromus inermis* to die out to the release of growth-inhibiting substances from its dead, decaying roots. According to Gries (1943a), the types of substances produced depend largely on the types of organisms that cause decomposition. Sterile extract from decomposed soybean plants was not toxic, but that from red clover was very toxic to strawberry and tobacco plants. When soybeans were sterilized and then decomposed by the organisms usually found on red clover, the extract was toxic; but the extract from red clover decomposed by soybean organisms was not toxic. Many of these decomposition products are toxic to fungi also, hence certain crop rotations may affect the prevalence of certain plant diseases. Juglone, obtained from walnut roots, is toxic not only to seed plants but also to certain fungi (Gries, 1943b). Bonner (1946) found that substances escaping from guayule roots are toxic to guayule seedlings, and Gray and Bonner (1948) discovered that the dead leaves of *Encelia farinosa* release a water-soluble substance which is toxic to tomato seedlings and probably to other plants.

It is generally considered undesirable to plant peaches on old orchard sites, because the new trees often grow poorly. Proebsting and Gilmore (1941) investigated this situation and decided that poor growth could not be attributed to pathogenic organisms or to depletion of minerals. They found that addition of peach roots to soil in which peaches had never been grown inhibited the growth of peach trees. The inhibiting substance was obtained from the bark by

ether extraction. Apparently, the possibility of injury from toxic materials released during decomposition of roots and other plant residues is of considerable importance. It is claimed that accumulation of such substances is least in well-aerated soils and that under favorable conditions they usually disappear in a few months. Childers (1941) states that corn seldom thrives on old orchard sites until after several years have passed. He suggests that this may be the result of the high concentration of arsenic from spray residues. Corn was shown to be rather sensitive to arsenic. Accumulation of arsenic and copper spray residues sometimes reaches toxic concentrations in orchard soils and in soils where arsenicals have been used as weed killers.

It is well known that artificial illuminating gas, or rather the ethylene contained in it, is injurious to plants. Roots of trees often are injured by leaks from gas mains (Deuber, 1936). According to Gustafson (1944), natural gas containing neither ethylene nor carbon monoxide is not harmful to plants. Tree roots sometimes are injured by industrial wastes and chemicals carelessly dumped on the soil. The author has observed the decline and death of several willow oak trees planted on soil containing large quantities of plaster that had been discarded during building operations. Apparently, injury resulted from the high pH, which reduced the availability of certain minerals. In California, injury occurred where dealcoholized waste from wine distilleries was dumped upon the ground and allowed to seep into orchards and vineyards (Proebsting and Jacobs, 1938). Death was caused not by toxic substances in the waste itself but by substances produced during anaerobic decomposition in the soil.

Mechanical Injury

Strong winds break many roots and injure the root systems of many trees that are not actually blown over. If the trees are healthy, such injury is doubtless soon repaired. During the construction of streets, sidewalks, and buildings,

root systems are often greatly reduced in extent. While growth of the tops is usually reduced, the frequency with which the trees survive indicates that the average root system is probably at least twice as large as is necessary for the survival of the trees. Elazari-Volcani (1936) found that more than 50 per cent of the roots of young citrus trees can be removed without serious injury. The author has observed pines which survived for a number of years, although approximately three-fourths of the soil mass and the root system was removed from the base of the trees. Weaver and Zink (1946a) state that removal of half or even more of the root system of several species of grasses had little harmful effect on growth. Some care is necessary in interpreting the results of root-pruning and girdling experiments on woody plants, because of the prevalence of root grafts. Roots of adjacent trees often grow together in such a manner that considerable cross transfer of water and food probably can occur. This might partially compensate for loss of part of the root system of an individual tree. The occurrence of cross transfer through root grafts probably also explains the prolonged survival of certain girdled trees.

Root systems of crop plants often are injured by too-deep or too-close cultivation. Various experiments in the corn belt have shown that cultivation of corn to the depth of 4 or 5 in. materially reduces the yield as compared with that of plots cultivated to the depth of an inch or less. In well-aerated soil, the best yields were obtained by removing the weeds without stirring the soil (Weaver and Bruner, 1927). Since corn develops numerous roots near the surface, it probably suffers more from cultivation than do some other crops. Cotton (Leonard, 1944) and tobacco (Gier, 1940) root systems usually are damaged by the methods of cultivation in common use. Exercise of care in the selection and use of cultivating equipment can largely obviate such injury. The drastic working of the surface soil required to throw up the basins and deep furrows used in orchard irrigation practically prevents the development of

roots in the upper foot of soil, particularly if cultivation is frequent.   This is unfortunate, because the highest concentration of mineral nutrients exists in the surface and better aeration also makes conditions most favorable for absorption of mineral nutrients.   Such shallow-rooted species as azaleas ought not be cultivated at all, because injury to the root systems is certain to occur.   Weeds can be controlled around such plants by mulching.

ROOT AND STEM PRESSURES AND EXUDATION PHENOMENA

The existence of positive pressure in plants and the exudation of sap from wounds has been known to man since before the beginning of recorded history. In the Far East, sap has long been obtained from palms to make sugar and wine; the first sugar known to Europeans probably was palm sugar from India. In Mexico, the Spanish conquistadors found the natives collecting the sugary sap of agave and fermenting it. The Indians of New England and adjacent Canada were tapping maple trees and boiling down the sap to make sugar before any European settlers arrived there. Exudation of sap from cut stems of the grape was mentioned by many early writers, and some of them speculated on the causes. The interest of various early scientists in sap flow and pressure phenomena has been mentioned in Chap. 1. Evelyn (1670), in his "Sylva," discussed the best methods of tapping birch and the uses of the sap, especially in making beer. According to Sachs (1882), it was not until the middle of the last century that the occurrence of exudation from the stumps of many cultivated plants was first demonstrated by Hofmeister. During that period, serious efforts to explain exudation phenomena began to be made by scientists.

Species Exhibiting Exudation

No recent attempts have been made to list the species from which exudation occurs, but it certainly does take place in scores, perhaps in hundreds, of species. Wieler (1893) collected from the literature references to "bleeding"

or "weeping" in 126 species, belonging to 93 genera and 47 families, distributed among the ferns, gymnosperms, and angiosperms. He added from his own observations 62 additional species. Apparently, Wieler indiscriminately included examples of exudation from glandular hairs, wounded stems, guttation, and other types of exudation, whether it was known to be caused by root pressure or not. Several conifers are included in his list, but so far as the writer is aware, no conifer exhibits true root pressure under normal field conditions. In a private communication to the author T. W. Daniel reported the occurrence of measurable exudation from stumps of several species of conifer seedlings growing in aerated culture solution. Wieler soaked the root systems of certain conifers in salt solution. When they were transferred to water, exudation occurred. This was recently repeated by Eaton (1943), who gradually increased to several times normal the concentration of the nutrient solution surrounding the roots of seedlings of *Cedrus deodara* and *Thuja orientalis*. After 8 days, this concentrated solution was replaced by tap water, and the seedlings were detopped. Appreciable exudation occurred from the stumps of these plants, but none took place from root systems that were kept in dilute nutrient solution. Exudation under such artificially produced conditions is not to be regarded as evidence that any occurs in those species under normal conditions.

There has been some debate concerning exudation in aquatic plants. Thut (1932) reinvestigated this problem and found that measurable quantities of sap exuded from cut stems of the several species studied. He believed this exudation to be caused by root pressure, because it is greatest in quantity in species which are well rooted and does not appear in those species which have few roots or none.

Clark (1874), when he tested over 60 species of trees and shrubs by boring holes into them, found appreciable exudation occurring from species of Acer, Betula, Juglans, Ostrya, and Vitis only, though slight exudation occurred from sev-

eral other species. It is well to remember, however, that failure to observe sap flow from one or two specimens is by no means conclusive evidence that it never occurs in a species. The time and amount of sap flow are affected by weather, season, and condition of the plant; hence extensive tests over a considerable period of time on a number of individuals are needed before generalizations can be made concerning a species. The reasons why some species show no exudation are unknown and ought to be carefully investigated. It may be for either anatomical or physiological reasons, and an understanding of this probably would aid us to explain most exudation phenomena.

Types of Exudation

Much confusion has resulted from failure to distinguish between exudation caused by root pressure, exudation caused by local stem pressure, and exudation from specialized secretory cells, such as those of glandular hairs. Wieler apparently treated all types of exudation as bleeding, although Clark (1875) and Sachs (1882) had already distinguished between exudation caused by root pressure and exudation caused by pressures developed locally in the stems. Exudation from sugar maple and from palms appears to be the result of locally developed stem pressures, while exudation from birch and from grape appears to be caused by root pressure. True guttation is caused by root pressure, but secretion of water or solution occurs also from glandular cells, independently of any pressure existing in the xylem sap. Many of these glandular structures are specialized epidermal hairs. This form of exudation is quantitatively unimportant, but the mechanism causing it is of considerable interest and deserves further study. Sometimes, also, there is a flow of sap from cut sieve tubes in the phloem of both woody and herbaceous species.

Occasionally pressures of a very different origin are observed in trees. For example, Abell and Hursh (1931) reported several instances in which gas pressure existed in

Quercus coccinea in late summer and early autumn. When increment borings were made, liquid dripped out, accompanied by a hiss, as of escaping gas. In one instance the core was blown out, and this was followed by a stream of liquid, which was thrown 3 or 4 ft. from the tree. Cores were also blown out of some trees of *Q. alba* and *Q. montana.* In certain instances, when the gas escaping from the holes was lighted, it burned with a blue flame for about 30 seconds before the pressure began to decrease. This gas came from trees having decayed heartwood and was probably produced by the organisms that were decomposing the wood. Several other examples of such phenomena have been published.

Flow of liquid from cracks and other wounds, called slime flux, is sometimes observed in trees. This seems to be associated with the activities of microorganisms. According to some investigators, slime flux is always associated with a water-soaked condition of the heartwood, known as "wetwood." Carter (1945) studied the occurrence of wetwood and slime flux in elm trees. He concluded that the wetwood, or water-soaked, condition of the central part of the trunk results from the activities of a bacterium. Gas and liquid pressures of 5 to 30 lb. were frequently observed, and once a pressure of 60 lb. was registered. Samples of gas from affected trees contained as much as 46 per cent of methane. The pressure forces sap out through cracks in the trunk and through pruning wounds, causing the slime flux. The exuding liquid comes from the heartwood of the tree, rather than from the ascending sap stream.

Exudation Caused by Stem Pressure

Maple Sap Flow. The best known example of exudation in North America is the flow of sap obtained by tapping maple trees. Although the sap of other species of maple also contains sucrose, practically all maple syrup and maple sugar are made from the sap of *Acer saccharum* and *A. saccharum nigrum.* The earliest careful investigation of the conditions governing maple sap flow seems to have been

made by W. S. Clark (1874, 1875), who published some of the best plant physiological observations made in America during his time. Clark reported that in Massachusetts sap flow might occur any time from early October to late April if a freezing night was followed by a warmer day with temperatures above freezing. The importance of freezing nights followed by sunny, warm days is well known to operators of sugar camps, because little or no flow occurs when the temperature is continuously above or below freezing. Because of this dependence on weather conditions, sap flow is usually intermittent, and from 2 or 3 to 10 or 12 "runs," or periods of sap flow, may occur in a single spring. Sap flow ceases in the spring when the night temperatures no longer fall below freezing. Daily fluctuations also occur, sap flow usually beginning in the forenoon, as the temperature rises, and ceasing in the afternoon. Jones, Edson, and Morse (1903), who studied maple-sap production in Vermont, stated that over 60 per cent of the total sap flow occurs between 9 A.M. and noon; the writer found that in North Carolina sap flow from *A. rubrum* usually ceases by late afternoon and is resumed the next morning if the temperature is high enough.

Gauges placed in holes bored in tree trunks have revealed that periods of sap flow coincide with periods of positive pressure. As might be expected, no sap flow occurs when subatmospheric pressures exist, as is usually the situation in late afternoon, at night, and early in the morning. Maple roots often show negative pressure, even when positive pressure exists in the trunk; and Clark reported that roots cut loose from the tree absorbed water, but no sap ever exuded from them. Jones, Edson, and Morse found slight positive pressures in maple roots but regarded them as too slight and fluctuating to be of importance in causing sap flow. Most, or perhaps all, of the sap comes from the sapwood, and the flow from above into a hole is much greater than the flow from below. While sap sometimes runs from broken twigs in a treetop, the flow usually is much greater from holes

bored near the base of the trunk. The largest quantity of sap usually is obtained from holes on the south side of trees, and the east side is second in yield, probably because these sides are most likely to be warmed up by the sun during the forenoon. A large tree is often tapped in two places.

The volume and the quality of sap produced depend on the tree and on soil and weather conditions. Maple trees grown as a source of sap should have the largest possible crown, instead of the long, clear stems favored for timber trees; hence stands should be kept fairly open. A large crown is needed to provide the photosynthetic surface required for producing a large quantity of sugar. Jones, Edson, and Morse reported that defoliation during the summer greatly reduced the yield of sugar the next spring. Trees well exposed to the sun generally produce more than those that are heavily shaded—another reason for maintaining fairly open stands. Obviously, trees on fertile, well-watered soil will yield better than those on infertile or dry soil. Dambach (1944) found the maple-syrup yield from an ungrazed Ohio woodlot to be substantially larger than that from an adjacent grazed woodlot. He attributed this largely to increased pore space in the soil and greater depth of litter, with consequent reduction in depth of freezing in the ungrazed woods, both of which favor vigorous tree growth. Bryan, Hubbard, and Sherwood (1924) state that the average yield is 10 to 20 gal. of sap per tree, but 40 gal. is sometimes obtained from a heavy-flowing tree. The sugar content has been observed to vary from 0.5 to 7.0 or even 10.0 per cent, but usually it is in the neighborhood of 2.0 to 3.0 per cent. It is estimated that 100 trees should produce about 40 gal. of maple syrup or 300 lb. of sugar.

The sugar represents carbohydrates accumulated during the summer in the wood, partly as starch and partly as sucrose and hexose sugar. The starch is largely converted into sugar during the early winter, resulting in a high sugar content during the late winter and early spring. Since this sugar exists in solution in the xylem, it readily drains out

with the sap if any internal pressure exists in the tapped tree. Such a flow has no relation to the normal translocation of carbohydrates or to the upward movement of sap in transpiring trees. Since relatively little sugar accumulates in the stems of most herbaceous species, very little occurs in the exudate.

Apparently the trees are little injured by tapping, since many healthy trees are known to have been tapped for several decades. Jones, Edson, and Morse estimated that less than 10 per cent of the total sugar in a tree was removed by tapping and concluded that this small loss would be injurious only if the following summer were very unfavorable for photosynthesis or if the tree were defoliated by insects.

It was long assumed that maple sap flow is caused by root pressure, but the observations of Clark and of Jones, Edson, and Morse indicate that this is not true. Recently, Stevens and Eggert (1945) presented further evidence that root pressure is not involved. They placed entire trunks and portions of trunks of small trees of *A. rubrum* in tubs of water and tapped them. Sap of normal composition was yielded by the isolated tree trunks and portions of trunk, as long as they were supplied with water and exposed to temperatures which fluctuated above and below freezing. The daily fluctuations in sap flow from the isolated tree trunks were similar to those of intact trees.

These observations ought to help dispel the widely held view that sap flow is associated with "the rise of sap in the spring," a phenomenon more often mentioned by poets than by plant physiologists. There really is no well-defined "rise of sap" in the spring until trees leaf out and transpiration begins, and by that time no sap can be obtained from tree trunks. There probably is little movement of sap in the trunk of a dormant maple tree until an outlet is provided by tapping. Then some upward movement of water from the roots occurs, replacing that lost through the wound.

Johnson (1945) attributed sap flow to the activities of

living cells and suggested that the beneficial effect of cold nights is principally because the cells are better supplied with oxygen, since it is more soluble in cold water. The author doubts whether oxygen supply has anything to do with maple sap flow. This could easily be determined by enclosing a section of tree trunk in a gas-tight container and displacing the oxygen with nitrogen. Stevens and Eggert believe that freezing at the surface of tree trunks causes movement of water toward the outer part of the wood, producing tension, which causes sap to move up in the tree until freezing stops further movement. When the sap is released by thawing, it flows out of any available opening. The sap pressures of an atmosphere or more which have been observed probably are caused by the gas and liquid pressure developed when the tree trunk warms up. When it cools down at night, contraction of the gas and liquid causes decreased pressure and cessation of exudation. Loss of water on dry, windy afternoons also sometimes produces the same effect. Absorption of water probably is increased by the decreased internal pressure. This pleasingly simple explanation of sap flow may prove inadequate in the light of further investigations.

Other Examples of Stem Pressure. In the warmer parts of the world, large quantities of sap are obtained from palms. This sap is gathered, usually by cutting off part or all of the inflorescence, though Hill (1937) states that sap is obtained from the stem of the date palm, somewhat as it is from a maple tree. Molisch (1902), who studied this process in Java, concluded that sap flow from palms is caused by forces originating in the vicinity of the wound. The flow can be prolonged by repeatedly cutting and pounding or otherwise wounding the stem, and it is said that a yield of 6 or 8 liters per day can be obtained for several months. This exudation is not caused by root pressure, because root pressure is seldom manifested in the lower part of the stems. The importance of this process is indicated by the fact that, according to Hill, 100,000 tons of palm sugar are produced

annually in India alone, and it is produced in many other tropical countries, as well.

In Mexico, large quantities of sap containing sucrose are obtained from the agave. The young inflorescence is cut out before it opens, and a cavity large enough to hold one to several liters is scooped in the top of the stem. Sap collects in this cavity and is removed daily, mostly to be fermented into pulque. A minimum of a liter per day is produced for 10 to 15 days, the yield depending somewhat on weather conditions. The tissue lining the cavity is periodically bruised during the period of sap flow, to maintain the flow, which may continue for many days. Sachs attributed this sap flow to root pressure, but there is a possibility that it is the localized result of wounding the parenchyma of the stem at a time when large quantities of sugar have been accumulated, prior to the flowering of the plant. According to MacCallum (1908), *Agave americana* flowers in Arizona in soil so dry that little or no water can be absorbed. Under such conditions, the water used by the growing inflorescence comes from the fleshy leaves, which shrink in size and decrease in dry weight during flowering. The entire plant dies after flowering. It is apparent that the causes of sap flow in agave ought to be investigated further.

Molisch (1902) regarded the stem pressures reported in woody stems by earlier writers as being caused by the activity of cells in the immediate vicinity of wounds, rather than by root pressure. MacDougal (1925, 1926) observed that considerable pressures were developed for a few days after holes were bored in cacti and in *Pinus radiata,* but that these pressures soon disappeared and negative pressure and absorption of water were often observed. He concluded that roots do not develop these pressures, but that they are caused by changes in permeability of cells adjacent to wounds, which allow their contents to leak out. It appears that we still have much to learn concerning the causes of exudation from wounds in stems and that the causes may be quite different in different species.

Exudation Caused by Root Pressure

Superficially, the exudation of sap from tapped birch trees seems similar to that from maples, but most of those who have compared the two processes have concluded that the exudation really is somewhat different in the two cases. In the birch it never occurs in the winter, but only in the spring after the temperature is continuously above freezing. By this time, maple sap flow often has almost or entirely ceased, and flow from birch continues later in the spring than flow from maple. The flow is much more steady than sap flow from maple, continuing day and night after the weather warms up, until the buds begin to open. Use of pressure gauges showed that in birch pressure develops first and is greatest at the base of the tree. In maple, positive pressure often exists in the trunk, while pressure in the roots is subatmospheric, and much greater fluctuations in pressure occur in maple than in birch. According to Clark, sap exudes into bore holes mostly from the upper side in maple, while in birch it enters from the lower side of the hole. Because of these differences, it is believed that exudation from birch is caused by pressure developed in the roots rather than in the stem. In the spring, as the soil warms up, water absorption begins and, since little water is lost by the bare branches, pressure develops. As soon as the leaves expand, transpiration begins to remove water, producing subatmospheric pressure in the water-conducting system and thereby preventing further exudation. The situation appears to be essentially the same in grape, also, where bleeding does not occur until the soil has warmed up. A careful survey ought to be made to determine in which species exudation is caused by root pressure and in which it results from pressure developed locally in the stem.

Volume of Exudate

The volume of exudate depends on the species and size of plant, on the ratio of absorption to transpiration, and on

various environmental factors—particularly, temperature and amount of available soil moisture. Sugar maples may yield 5 to 6 liters of sap per day and 25 to 75 or even 150 liters in a season. Betula and Ostrya are said to yield even greater volumes of sap than maple does. A paper birch 37.5 cm. in diameter produced 28 liters of sap in one day and 675 liters during the season, according to Clark. Johnson (1944) reported yields varying from less than 20 to over 100 liters from white birch (*Betula papyrifera*) trees 8 to 17 in. in diameter. The volume of sap produced was not proportional to the size of the tree, as some small trees produced more sap than some of the large ones. Weller (1931) observed sugar cane stools to exude over 400 ml. of sap in 24 hours and 1,000 ml. during the first week after detopping, while corn plants detopped in the milk stage yielded over 500 ml. of sap in 3 days and over 1,700 ml. in 15 days (Lowry and Tabor, 1931). Sachs mentioned a sunflower plant about 3 m. in height, with a stem diameter of 4 to 5 cm., which exuded 1,061 ml. of sap in 13 days—a volume of sap about three times the volume of the entire root system. Crafts (1936) transferred squash plants grown in nutrient solution to tap water and cut off the tops. Four of them yielded 550 ml. of sap in 24 hours, though the total fresh weight of their root systems was only 450 gm. The volume of sap exuded in 24 hours was greater than the total volume of the root system and was estimated to be more than five times the volume of the lumina of the xylem vessels. Sperlich and Hampel (1936) found the volume of exudate from sunflower root systems increased with their age until flowering occurred, and then decreased.

Composition and Osmotic Pressure of Exudate

The liquid that exudes from cut stems and hydathodes is not pure water but contains varying proportions of carbohydrates, nitrogenous materials, organic acids, and mineral salts. Maple sap contains about 3 per cent of sucrose; small amounts of glucose and proteins; some minerals, especially

calcium and potassium salts; and organic acids, especially malic acid (Jones, Edson, and Morse, 1903). The sugar content of birch sap is only about half that of maple sap; and according to Johnson, white birch sap contains a mixture of reducing sugars with fructose predominating, while yellow birch contains approximately equal quantities of glucose and fructose and a small amount of sucrose. The pH of both birch and maple sap was found by Johnson to range from 6.8 to 7.6. Priestley and Wormall (1925) analyzed grape sap and found it to contain 1.56 per cent of solids—of which 0.56 per cent was ash, an equal amount was organic acids, 0.33 per cent was reducing sugar—plus a small quantity of organic and inorganic nitrogen. Weller (1931) published analyses of sap from sugar-cane stumps, Pierre and Pohlman (1933b) summarized the analyses of several investigators, and Anderssen (1929) cited data on woody species. Most of these analyses were based on sap exuding from cut stems.

The composition and osmotic pressure of sap exuding from the stumps of herbaceous species varies somewhat with the composition of the solution surrounding the roots. It was observed by van Overbeek (1942) that the osmotic pressure of xylem sap from tomato root systems in full-strength Hoagland solution averaged 1.3 atmospheres, while that from root systems in distilled water averaged only 0.4 atmospheres. Eaton (1943) reported that, as the concentration of the solution surrounding the root systems of cotton plants was increased, the osmotic pressure of the xylem sap increased from 0.9 to 3.0 atmospheres. The xylem sap from squash plants was observed by Stocking (1945) to have an osmotic pressure of about 1.9 atmospheres. Maximov (1929) gives values ranging from 0.36 to 1.46 atmospheres for the xylem sap of several herbaceous species. Apparently, the osmotic pressure of xylem sap normally is less than 2 atmospheres. Apparently, salts constitute most of the solutes in the root xylem of most herbaceous plants. Skoog, Broyer, and Grossenbacher (1938) found no appre-

ciable amount of sugar in the exudate from sunflower stumps, and van Overbeek (1942) found no sugar in exudate from tomato stumps, except for a short period after detopping, when sugar may have escaped from the phloem.

Several workers have investigated the possibility of analyzing the sap that exudes from the stumps of detopped plants and using the results as a guide in determining the fertilizer needs of the plants. Lowry and Tabor (1931) reported that the xylem sap obtained from stumps of corn plants had a composition much nearer that of the soil solution than does sap expressed from the plant tissues. According to Pierre and Pohlman (1933a), sap exuded from stumps of herbaceous plants gives a good measure of phosphate supply and probably is a satisfactory indicator of the supply of available nitrogen and potassium. Lowry, Huggins, and Forrest (1936) found that the addition of various elements to the soil usually produced increases in their concentration in the xylem sap. Weller (1931), on the other hand, reported considerable discrepancies between the composition of the exudate from sugar cane and the composition of the soil extract. Lauritzen (1934) suggested that samples of soil solution might be obtained by displacing it through plant root systems with air pressure. Samples of soil solution can now be obtained with greater precision by using the pressure-membrane equipment described by Reitemeier and Richards (1944).

Since sap exudes from stems of most woody species for only a limited time in the spring, attempts have been made to obtain samples at other seasons. Atkins (1916) obtained sap by centrifuging pieces of stem. Bennett, Anderssen, and Milad (1927) found it possible to displace samples of sap from twig segments by both gas and liquid pressure. They preferred a 0.02N potassium chloride solution to water as a displacing agent, because it was easier to determine when all the sap had been displaced by the sudden change in conductivity. Use of gas pressure obviated the danger of contamination which exists with liquid displacement, but it is

difficult to force gas through the moist cross walls at low pressure. Sap centrifuged from the xylem of twigs of several species in Ireland had osmotic pressures of about 0.5 to 1.5 atmospheres, according to Dixon and Atkins (1916). In general, the concentration of solutes was highest in early spring, was very low during summer and early autumn, increased slowly during the winter, and suddenly reached its peak again in the spring. Similar changes in concentration were observed in xylem sap extracted by air pressure from apricot and pear twigs in California, though the concentration was lower (Anderssen, 1929).

Shear and Wingard (1944) suggest that the composition of the xylem sap may affect the susceptibility of plants to certain diseases of the vascular system. When potassium is deficient in the soil, it is low in the conducting system also, while phosphorus and nitrate nitrogen may be high. Under such conditions, wilt of corn is much more severe, possibly because growth of the fungus causing the disease is favored by the excess of nitrogen in the xylem sap.

Magnitude of Root Pressure

The first measurements of root pressure known to the writer are those of Hales, who observed a pressure of more than one atmosphere in grape. Pressures of 2.6 atmospheres have been reported for birch in New England by Clark (1874) and by Merwin and Lyon (1909). The maximum pressure observed by Weller in sugar cane was 1.9 atmospheres. The most drought-resistant varieties maintained the highest pressures during periods of decreasing soil moisture. White (1938) reported that excised tomato roots growing in culture solution developed pressures in excess of 6 atmospheres—probably equal to at least 10 atmospheres. These, which are probably the highest root pressures ever recorded, are the more remarkable because they were produced by pieces of root only a few centimeters in length and less than 1 mm. in diameter. Boehm (1892) and Figdor (1898) observed pressures of over 8 atmospheres in stems

of woody plants, but Molisch claimed these pressures were of local origin—not really root pressure. Boehm attached manometers to holes bored in Aesculus and Tilia and left them for long periods of time. The high pressures were developed in the spring, the highest recorded being one of 8.64 atmospheres. Figdor's work was done on trees in Java, where the pressures usually were from 4 to 6 atmospheres, but one of 8.2 atmospheres was observed. Molisch himself observed pressures up to 6.4 atmospheres in *Juglans regia*. MacDougal (1926) observed a pressure of 4 atmospheres in *Pinus radiata*, but he attributed this to locally developed forces rather than to root pressure. Sabinin (Maximov, pages 53–55) by indirect methods calculated the exudation pressures of various herbaceous species to range from 0.5 to 1.5 atmospheres.

The amount of exudation and the pressure developed depend not only on the kind and condition of the plant, but also on the environment. No exudation occurs from root systems in cold or dry soil or from those in poorly aerated media. The effects of temperature, aeration, and moisture content are discussed in Chaps. 8 and 9, in connection with the active absorption mechanism. Observations by van Overbeek (1942) showed that the root pressure of plants grown in full-strength Hoagland solution was higher than that of plants grown in half-strength solution. The average root pressure observed in dilute solution was about 1.4 atmospheres, while the maximum observed in full-strength culture solution was 3.5 atmospheres. Eaton (1943) observed similar increases when root systems were grown in concentrated solutions. This probably was because of a higher salt concentration in the xylem of the plants grown in the more concentrated solution.

Leonard (1944) observed that injury to cotton roots by cultivation caused a marked decrease in root pressure. He therefore used reduction in root pressure as an indication of the amount of injury caused by various cultural methods.

Periodicity of Exudation

Ever since the phenomenon was first observed by Hofmeister (1862), investigators have noticed fluctuations in magnitude of root pressure and volume of exudate, which seem to occur independently of variations in environmental
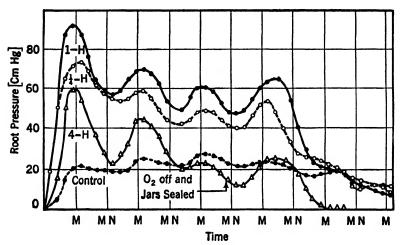
FIG. 24. Diurnal periodicity in root pressure and effects of aeration and concentration of the medium in which the roots were immersed. Plants in full-strength Hoagland solution (1-H) showed highest pressure, those in fresh one-fourth-strength Hoagland solution (¼-H) less, and those in four times the usual concentration (4-H) showed a rapid decrease in pressure. The control group was left in the one-fourth-strength Hoagland solution in which it had been grown. Need for aeration is shown by the fact that, when the containers holding the root systems were sealed, the pressure fell rapidly in all groups. (*From Grossenbacher, 1939.*)

factors. White (1938), observed a daily variation in pressure developed by tomato roots growing in nutrient culture. Grossenbacher (1939) reinvestigated this problem, controlling environmental conditions very carefully. He found a well-defined periodicity in rate of exudation of sunflower plants, with a maximum during the day and a minimum at night (see Fig. 24). When plants were grown with artificial light, supplied only during the night, the cycle was shifted so that the maximum came during the artificially

produced light period.   Under these conditions the cycle was controlled by the light and dark periods and was little affected by the time of detopping or minor fluctuations in temperature.   Plants grown with continuous artificial light also showed a 24-hour cycle in rate of exudation, but the time of occurrence of maxima and minima was determined by the time at which the tops were removed.   Skoog, Broyer, and Grossenbacher (1938) were unable to show any diurnal changes in respiration which could be related to the changes in exudation, and the causes of the periodicity remain unknown.   Sperlich and Hampel (1936) observed that the daily periodicity of exudation from sunflowers did not begin until more than 2 weeks after germination and increased with age up to maturity.

Rosene (1941) observed considerable variations in volumes of water absorbed and exuded by onion roots and segments of root.   The ratio of absorption to exudation was quite variable at first, but usually reached unity within 24 hours.   Such evidences of periodicity and variability are difficult to reconcile with a simple osmotic explanation of root pressure.

Possibly there is some relation between the periodicity in exudation and the rhythmic fluctuations in transpiration of coleus cuttings observed by Montermoso and Davis (1942). They observed a definite maximum about noon and a minimum at night in cuttings that were transferred to continuous darkness, with constant temperature.   After the cuttings were illuminated at night and kept in darkness during the day, this rhythm was reversed, so that the plants when placed in continuous darkness then showed the maximum at night and the minimum during the day.

Tissues Involved

Ordinarily it is assumed that whatever pressure is developed in the root is exerted through the water in the xylem and that the flow of sap comes from the xylem elements. This view was challenged by James and Baker (1933), who

claimed that sap flow occurs from the phloem of *Acer pseudoplatanus* and that the sap in the xylem actually is under tension rather than pressure. They based this view on various experiments with dyes. In one series, when dye was placed in holes bored in stems showing exudation and was left for 2 to 8 days, it was found to have penetrated both upward and downward in the xylem from the holes. It appears that these investigators misinterpreted their results, because they failed to take into account the marked diurnal variations in sap flow caused by the alternation of positive and negative pressures in the water-conducting system of woody plants. During the period of their experiment, subatmospheric pressure must have occurred in the stems on several occasions, causing the dye to be sucked back into the stems; yet at the beginning and at the end of the experiment, sap could be seen exuding from the test holes. Nevertheless, the statement of James and Baker caused this problem to be reinvestigated both in Europe and in America, to make certain that something had not been overlooked. Huber (1934) stated that sap certainly exudes from the xylem in *Sanchezia nobilis,* and Ingold (1935) found the same to be true of *Betula alba.* Crafts (1936) also observed that sap exudes from the xylem of several species of herbaceous plants. The author (Kramer, 1940c) found positive evidence that sap flow in the spring from wounded *Acer rubrum, Betula nigra,* and *Carpinus caroliniana* occurs only from the xylem. Observation of the stumps of several species of herbaceous plants under a dissecting microscope showed water exuding from the xylem but not from the region of the cambium or the phloem.

It is true that exudation does sometimes occur from the phloem of certain species, but it is small in quantity and unlikely to be confused with xylem exudation. Dixon (1933) reported that exudation was observed from the sieve tubes of over 40 woody species. Moose (1938) also observed exudation from the phloem of several woody species, even at times when subatmospheric pressures existed in the xylem.

At Ithaca, New York, phloem exudation did not occur in the spring but began late in June and was most abundant on sunny days in late summer. Crafts (1936, 1944) and others have studied phloem exudation of cucurbits, and Huber (1937) and his associates attempted to study translocation of organic substances in trees by analyzing phloem sap. Crafts decided that the phloem exudate from cucurbits is not a representative sample of the material normally being translocated through the phloem, though the exudate from woody species may be.

Guttation

The most common and conspicuous manifestation of root pressure is the exudation of drops of liquid from the edges and tips of leaves. This phenomenon, which was often called "weeping" by the earlier writers, was first termed guttation by Burgerstein in 1887. He reported that it occurs in 333 genera belonging to 115 families (Burgerstein, 1920); to these Frey-Wyssling (1941) added 12 genera. The latter authority regards it as a general phenomenon of growing plants, both woody and herbaceous, occurring whenever absorption exceeds transpiration.

Guttation ordinarily occurs through hydathodes—stomate-like pores in the epidermis—below which are intercellular spaces surrounded by thin-walled parenchyma cells. The xylem of a small vein terminates beneath each hydathode, and apparently root pressure forces water out of the xylem, flooding the intercellular spaces and causing an overflow through the pores to the exterior of the leaf. Guttation occurs also through ordinary stomates of some grasses and legumes; and, according to Sachs, drops of water sometimes exude from epidermal cells where no stomates occur. Haberlandt (1914) distinguished between epithem hydathodes, from which water is forced by root pressure, and active hydathodes, from which water is secreted by forces developed in the cells themselves. It seems preferable to term the latter "glands," and the outflow of liquid "secretion," re-

serving the term hydathode for the stomatelike structures from which water is forced by root pressure. Lepeschkin (1923) discussed various types of exudation from plant hairs and other glandular structures in which root pressure is not involved and in which exudation may occur even from somewhat flaccid plants. In addition to water, glands frequently secrete other substances, such as sugar, salts, enzymes, resins, and volatile oils.

Examples of exudation from uninjured woody stems have been reported. Raber (1937), in Louisiana, observed sap flow from leaf scars of deciduous trees after the leaves had fallen in the autumn; and Friesner (1940), in Indiana, observed exudation of sap from uninjured stems of stump sprouts of *Acer rubrum* in February. This exudation probably occurred from lenticels. Raber termed such phenomena guttation.

While most plants exude only a few drops of water during a night, species of Colocasia have been reported to exude from 10 to 100 ml. in a single night. Dixon and Dixon (1931) state that the guttation fluid of *Colocasia antiquorum* is almost pure water, but that guttated liquid usually contains measurable quantities of solutes. These include both organic and inorganic compounds (Wilson, 1923). The drops of water exuded either roll off, evaporate, or are drawn back into the leaf as the xylem pressure decreases. The liquid sometimes contains so much solute that when the water evaporates a noticeable deposit is left on the leaves. For example, the leaves of certain saxifrages become coated with calcium (Schmidt, 1930), and Curtis (1944a) found the leaves of plants on a heavily fertilized lawn encrusted with glutamine. Eaton (1943) reported the concentration of solutes in the exudate from hydathodes of cotton plants grown in a solution of low concentration to have an osmotic pressure of only 0.13 atmosphere, while that from plants in a culture solution of normal concentration ranged from 0.51 to 0.90 atmospheres. He suggested that concentration of solutes in the exudate is reduced below the concentration

occurring in the root, because the salts are removed from the xylem in the roots and in the stems and leaves. As a result, the concentration of exudate from the hydathodes would be lower than that of exudate from a stump. In his experiments, the stump exudate was about three times as concentrated as the hydathode exudate.

According to Curtis (1943) and Ivanoff (1944), injury to the edges and tips of leaves of various herbaceous species sometimes results from the high concentration of salts left by the evaporation of guttated water. The salts either remain on the surface or are redissolved and drawn back into the leaf, where the high concentration causes injury to the mesophyll cells. It is suggested that many instances of tip-burn are caused in this manner. Curtis (1944b) believes that guttation water can redissolve spray materials from the surface of the leaf and draw them back into the interior, causing injury to the cells. Johnson (1936) suggests that guttation may cause water-soaking of the leaves, facilitating the entrance of pathogenic organisms which otherwise would have difficulty in gaining entrance. This might explain occasional epidemics of leaf diseases following periods of soil and weather conditions that are favorable to guttation.

Investigations by Montfort (1920) and by Woodhouse (1933), among others, substantiate the long-held view that guttation is caused by hydrostatic pressure originating in the roots. Montfort (1922) regarded it as a sensitive indicator of the availability of water to plants and used it thus in his studies of the water relations of bog plants. Gäumann (1938) also considered it a measure of root activity. The writer has observed, however, that plants showing no guttation in the morning sometimes will reveal exudation as soon as the tops are removed; hence failure to observe guttation is not conclusive evidence of the absence of positive pressure in the roots and lower part of the stem.

Guttation is most common in plants that grow in moist, warm soil, with their tops surrounded by humid air. This is

because it occurs only when absorption is sufficiently in excess of transpiration to cause development of a positive pressure in the water-conducting system. Conditions which hinder water intake—such as poor aeration, cold or dry soil, a high concentration of solutes, or the presence of toxic substances—and conditions which favor high transpiration reduce or prevent guttation. Raleigh (1946) found that plants deficient in nitrogen, phosphorus, potassium, calcium, or magnesium never showed guttation; but that when the deficiency of nitrogen, phosphorus, or potassium was eliminated, guttation began within 24 hours or less. Plants deficient in calcium or magnesium failed to guttate when these elements were added to the culture solution, probably because permanent injury had occurred. Since the proper combination of conditions most often exists at night, evidence of guttation is usually most abundant in the early morning. Much of what is usually regarded as dew, particularly the drops of water on the tips of grass blades, is really guttated water. The importance of guttation in the life of the plant is doubtful. Curtis (1944a) believes that it affords a sort of safety valve, to regulate turgor; but the mechanism of absorption is such that there is little danger of developing excessive turgor pressures.

Importance of Sap Pressure

There has been considerable discussion concerning the importance of sap pressure in plants. It has been argued that since pressure is developed regularly in a number of species it must serve some useful purpose. The writer sees no reason why the occurrence of a process or a structure is necessarily evidence of its usefulness. Various structures and processes which are neither beneficial nor harmful have doubtless survived during the evolution of present-day forms of plant life, simply because they did not hinder survival of the plant. Furthermore, the process of transpiration, although it is often distinctly harmful, has survived, because

it is the unavoidable result of a plant structure that is favorable to photosynthesis.

It has been claimed sometimes that sap pressure is important in refilling empty water-conducting vessels and in supplying opening buds with water and nutrients. There is a rather general belief that the "rise of sap" in the spring is in some manner related to the opening of buds, although no real evidence for this has ever been presented. As a matter of fact, no sap pressure is ever observed in many species, yet they seem to thrive; and in those species in which sap pressure does occur, it usually begins to disappear as the buds begin to open. Burstrom and Krogh (1946, 1947), who investigated the role of sap pressure in the opening of buds, reported that, while the development of buds in *Carpinus betulus* starts during the bleeding season, it proceeds very slowly as long as the bleeding lasts. They concluded that sap movement associated with bleeding could not supply the nutrients used by opening buds, but that there probably is a migration of ions to the buds, which absorb them from the sap much as the roots absorb ions from the soil solution. These investigators regard the occurrence of sap pressure as an osmotic phenomenon, resulting from the high concentration of sap in the xylem. No movement of sap is believed to occur in intact nontranspiring trees, and exudation is regarded as an artifact caused by wounding.

In conclusion, it seems probable that the occurrence of sap pressure is the fortuitous result of a particular combination of structure and physiological function that occurs in certain plants. Since many species never exhibit pressure and since in other species variations exist between individuals, it apparently makes no difference to the success of a plant whether or not sap pressure is developed.

CHAPTER 8

PROCESSES CONCERNED IN WATER ABSORPTION

Conditions in the water-conducting systems of rapidly transpiring plants are quite different from those which exist in slowly transpiring plants. During periods when the soil is moist and when little transpiration is occurring, water in the xylem is often under positive pressure, as is indicated by the occurrence of guttation and the exudation of sap from cuts made into the xylem. When transpiration is moderate to rapid or even when it is slow, if the soil is dry, the water in the xylem is under reduced pressure or, frequently, even under a tension. At such times, no guttation occurs and water is absorbed through stumps and wounds extending into the xylem, instead of exuding from them. This is easily demonstrated by cutting into the stems of transpiring plants under a dye solution, when it will be found that the dye rushes upward and downward almost instantaneously in the stems to a considerable distance, clearly staining the xylem.

Active and Passive Absorption

The existence of these differences suggests that the intake of water may be caused by at least two different groups of forces, which probably often operate quite independently of each other. Water absorption by slowly transpiring, well-watered plants appears to be caused principally by forces which are developed in the roots themselves. The living cells either maintain conditions favorable to osmotic movement of water, or by the expenditure of energy cause non-osmotic movement of water across the cortex and into the

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xylem; possibly they do both. Water intake by rapidly transpiring plants and by plants rooted in dry soil appears to be caused largely—perhaps, even entirely—by forces originating in the shoots and transmitted through the water in the xylem to the roots. It, therefore, seems desirable to discuss separately the water intake caused by these two different forces.

Some of the earlier modern physiologists, such as Sachs, Pfeffer, and Strasburger, made such a distinction either implicitly or explicitly; and Hales distinguished between root pressure and absorption by transpiring plants. Renner (1912, 1915) clearly distinguished between absorption caused by forces originating in the roots and absorption caused by forces originating in the transpiring shoots; he termed the two types "active" and "passive" absorption. Absorption of water under conditions resulting in the development of root pressure and guttation certainly occurs as the result of conditions maintained by the activity of living cells in the roots, hence it was called active absorption. Absorption by freely transpiring plants can occur through anesthetized or dead roots, or even in the absence of roots. The role of the roots, therefore, appears to be that of a passive absorbing surface; accordingly, the process was called passive absorption. Since Renner's terminology is fairly well established in the literature, it will be used in this discussion.

Active Absorption and Root Pressure

No plant process has provoked more discussion and controversy than has the problem of the causes of root pressure and its associated phenomena. This may have resulted in part from attempts to explain such unrelated phenomena as secretion from nectaries and glands of insectivorous plants in the same manner as guttation and exudation from detopped root systems. It also results in part from the fact that we still do not understand fully the nature of the forces concerned in water intake by individual plant cells; hence,

we can scarcely expect agreement concerning the nature of the water-absorbing mechanism of the root system.

The numerous explanations of active absorption and the resulting root pressure can conveniently be classified into two groups. One assumes the existence of some sort of secretory activity on the part of the living tissues of the roots. The other assumes that the process is a relatively simple one of osmosis, the living cells simply providing the differentially permeable membranes necessary for its functioning.

Secretory or Vital Theories of Root Pressure. One of the earliest definite theories involving secretory activity of the roots was that of De Candolle (1832). He believed that the root tips, which he termed "spongioles," were contractile organs which sucked in water and forced it into the xylem. His theory somewhat resembles that of Bose (1927), which appeared nearly a century later. Bose claimed that "the absorbing root-cells are continually stimulated by mechanical friction against the soil, giving rise to peristaltic waves of pulsation along the active propulsive layer of the inner cortex." This explanation seems as vague and unsatisfactory as that of De Candolle. According to Molisch (1929), slight rhythmic contractions of stems can be observed—at least under certain conditions. There is no evidence, however, that these contractions can move water or develop noticeable pressures. Hofmeister (1862) believed that absorption of water by the parenchyma of the root resulted in the development of turgor pressure, which forced water out into the intercellular spaces of the stele and into the xylem elements.

The possibility of differences in permeability of the inner and outer sides of the cells of the roots, resulting in secretion of water into the xylem, was discussed by Frey-Wyssling (1929), Lepeschkin (1906), Pfeffer (1897), Wieler (1893), and others. It was believed that the living cells of the roots were more permeable to water on the inner than on the outer sides, and that hence, as they absorbed water from

the soil and developed turgor pressure, the water moved inward and finally was forced into the xylem under pressure. Ursprung (1929) claimed that the suction tension (diffusion-pressure deficit of Meyer) was greater on the inner side than on the outer side of the endodermal cells and that the same was true of the vascular parenchyma. He stated that the "endodermis operates like a suction pump and reduction valve," and the "parenchyma of the bleeding root acts like a force pump." If true, this would cause a movement of water across the endodermis and into the stele. If such a difference in diffusion pressure exists, it can be maintained only by means of expenditure of considerable energy on the part of the endodermal cells, because water movement itself would tend to equalize any difference in diffusion-pressure deficit.

Several investigators have suggested that electroosmosis might be the cause of root pressure. It is well known that liquids can be caused to move through a membrane under the influence of an applied electric current. The volume of flow is proportional to the difference in potential, and the direction of flow is toward the pole with the same polarity as the membrane. Since cellulose and wood membranes in contact with water are negatively charged, water moves toward the negative pole. If the tissues in the stele have a lower potential—that is, if they are negative to the tissue of the cortex—then water should move inward across the root. Staining experiments by Bakhuyzen (1930) and by Keller (1930) indicate that the inner surface of the endodermal cells is negative to the outer surface, which would point to a difference in potential favorable to the occurrence of electroosmosis. Stern (1919) caused water to move through segments of willow twigs by producing a difference in electrical potential between the two ends, and movement across membranes of wood has been studied by Stamm (1928). Lund (1931) found differences in potential in woody stems that he believed to be great enough to cause inward and upward movement of water and the development of root pressure.

After careful review of previous work and some experimentation of his own, Heyl (1933) concluded that root pressure is not caused by a simple osmotic process, but probably is produced by an electroosmotic process, in which a potential difference is maintained by means of energy released by respiration of the root cells. On the other hand, van Overbeek (1942) quotes Blinks as considering it unlikely that electroosmosis is important, because the salt concentration in plant cells is unfavorably high for electrokinetic phenomena. Lundegardh (1944) also concluded that electroosmosis cannot be the cause of root pressure, because improbably high potentials would be required. Studying electrical potentials of wheat roots, he found the maximum difference between surface and interior to be only about 100 millivolts, while he calculated that a difference of 150,000 millivolts would be necessary to lift water 1 m.

Disagreement exists among physiologists concerning the relation between water absorption and rate of respiration. Newton (1925) observed that barley respired more in absorbing water from solutions of high osmotic pressure than in absorbing it from solutions of low osmotic pressure. Henderson (1934) also claimed that there was a correlation between the evolution of carbon dioxide, the absorption of oxygen, and the absorption of water by corn roots, which would indicate that the absorption of water is accompanied by the expenditure of energy. Wilson and Kramer (1949), on the other hand, found no correlation between respiration and water absorption by tomato roots, and concluded that Henderson's data showed no correlation either. Loweneck (1930) found that increases in transpiration and, consequently, in absorption of water by corn and *Sonchus oleraceus* were accompanied by no increase in root respiration. He decided, therefore, that absorption of water and root respiration are not interdependent. Skoog, Broyer, and Grossenbacher (1938) found no correlation between the rate of respiration and the rate of exudation from detopped root systems.

During the past decade, interest in secretion theories of root pressure has been renewed by claims that the cytoplasm actually "secretes" water into the vacuoles of cells.   It is not at present understood just how cytoplasm might bring about water movement into the vacuoles; therefore, we use the term "secrete" as a convenient means of partially concealing our ignorance behind an impressive word.   Bennet-Clark, *et al.* (1936) and Mason and Phillis (1939) reported that the osmotic pressure of sap expressed from several kinds of plant tissue, as determined cryoscopically, was considerably lower than the osmotic pressure of the solutions required to plasmolyze the same kinds of tissue.   Lyon (1942) found a similar situation to exist in potato tubers.   This led to the conclusion that some sort of nonosmotic force is concerned in the absorption of water by plant cells and tissues.   There is other evidence for the dependence of water intake on the physiological activity of the protoplasm.   Reinders (1938), Commoner, *et al.* (1943), and van Overbeek (1944) found that auxin increases the water intake of potato tissue; and Reinders found that water was absorbed only by well-aerated tissue.   Reinders believed that auxin increases water intake because it increases respiration, while Commoner thought that it increased the absorption of salts and that the increased concentration of solutes in the vacuole caused the increase in water uptake.   It was shown by van Overbeek (1944) that the concentration of the cell sap is not increased by auxin, and he concluded that its effect probably is on the respiratory mechanism regulating the nonosmotic water intake of the tissue.   Showacre and du Buy (1947) claim that the effect of auxin in bringing about cell elongation is caused by auxin-enhanced water intake, combined with auxin-increased extensibility of the cell walls.   Thomas and Hartley, working in the author's laboratory, found that potassium cyanide reduces respiration and water absorption of bean carpels and water absorption of potato tuber.   Wilson found that very dilute chloroform, which is supposed to increase respiration, also increased water absorption of immature

cotton seeds, the increase being greater in the presence of sugar than in its absence. In general, the available data indicate that water absorption by isolated pieces of plant tissue is increased by factors favoring high respiration, such as good aeration and auxin, but is decreased by factors decreasing respiration, such as cyanide and poor aeration.

Currier (1944) verified the existence of a discrepancy between the osmotic pressure of expressed cell sap, measured cryoscopically, and its osmotic pressure as measured plasmolytically in intact cells. He attributed this to contamination of expressed vacuolar sap by sap from the protoplasm and questioned the existence of a nonosmotic force in the uptake of water by plant cells. Eaton (1943) has energetically opposed the idea of a nonosmotic force's being concerned in absorption of water by cells. He attributes the discrepancy between cryoscopic measurements of expressed sap and plasmolytic measurements of intact cells to accumulation of solutes by the cells from the plasmolyzing solutions used in the tests. The writer doubts whether water uptake by plant cells and tissues can be explained completely on a purely osmotic basis. Levitt (1947) calculated that beet cells would be unable to supply enough energy to maintain a nonosmotic force of 5 atmospheres, as reported by Bennet-Clark. He believed, however, that it is quite possible for a root to maintain a nonosmotic gradient from epidermis to stele of 1.5 atmospheres, as suggested by van Overbeek.

There is considerable evidence that the active absorption mechanism of a root system behaves much like the absorption mechanism of individual cells. It is well known, for example, that root pressure, like water absorption by isolated pieces of tissue, is reduced or stopped by low temperature, poor aeration, and various toxic substances. Skoog, Broyer, and Grossenbacher (1938) found that auxin increases the rate of exudation of sunflower and pea plants, just as it increases the water intake of pieces of potato tissue. Rosene (1944) found that absorption and exudation of isolated onion roots was inhibited by dilute solutions of potas-

sium cyanide, and van Overbeek (1942) found that the root pressure of detopped tomato root systems was greatly reduced by potassium cyanide. According to van Overbeek, also, the osmotic pressure of the mannitol solution in which detopped root systems must be immersed to stop exudation was considerably greater than the osmotic pressure of the sap exuding from the stumps. He concluded that the force with which water is absorbed by detopped root systems consists of two components, an "active" or nonosmotic force, which is reversibly inhibited by dilute potassium cyanide, and an osmotic force, which is not affected by potassium cyanide. Root systems of low-salt tomato plants kept in distilled water developed a root pressure of 1.4 atmospheres, of which about 70 per cent could be inhibited by potassium cyanide. Root systems of high-salt plants kept in full strength Hoagland's solution during the tests developed an average root pressure of 2.68 atmospheres, of which about 50 per cent was "active," or inhibited by potassium cyanide, and about 50 per cent was osmotic, or not inhibited by potassium cyanide.

It has been suggested that there may really be no osmotic component, and that potassium cyanide does not completely inhibit exudation simply because it does not completely inhibit respiration. The existence of an osmotic component is indicated, however, by the fact that roots with a high salt content develop a higher root pressure than do roots with a low salt content, and that a smaller percentage of the total pressure is inhibited by potassium cyanide. On the other hand, some investigators deny the existence of any nonosmotic component in root pressure. It is obvious that these differences in viewpoint will not be resolved until the processes involved in water intake of individual cells are better understood.

Osmotic Theories of Root Pressure. Our present views on plant-water relations are still strongly influenced by the pioneer work of Dutrochet, who developed a theory of osmosis and applied it to various plant processes. He was

rather vague concerning the manner in which root pressure is developed, and most botanists of the nineteenth century and the early part of the twentieth century preferred some explanation based on differential permeability and secretion of water into the xylem. This was at least partly because they did not understand how water could move from the living parenchyma cells into the dead xylem elements. It was assumed that water could move only along gradients of increasing osmotic pressure. Therefore, it was difficult to understand how water could move from the living cells surrounding the xylem, which have an osmotic pressure of several atmospheres, into the xylem elements, whose contents usually have an osmotic pressure of only 1 or 2 atmospheres. Through the work of Blackman (1921), Thoday (1918), Ursprung (1929), and others, we now understand that water moves in plant tissue along gradients of diffusion-pressure deficit, which may be largely independent of the relative osmotic pressures of the cells. (Diffusion-pressure deficit is equivalent to such terms as suction force, suction tension, effective osmotic pressure, etc., used by various writers. See Meyer, 1938, 1945.) If the intervening cells are turgid, water can move across a tissue having high osmotic pressure to a region that has lower osmotic pressure but higher diffusion-pressure deficit. The writer found (Kramer, 1932), for example, that water would diffuse across a living, multicellular membrane with an average osmotic pressure of 9 atmospheres when it separated pure water from a sugar solution having an osmotic pressure as low as 2 atmospheres.

The first application of this principle to an explanation of root pressure seems to have been that of Atkins (1916), who stated (page 203) "that the inflow of water from the ground to the elements of the wood of the roots takes place across the cortical cells of the roots. For, though the latter have a much higher osmotic pressure than have the tracheae, they function merely as a complex semipermeable membrane, as they are already fully distended." Atkins suggested that the adjacent parenchyma cells secrete sugar into the xylem

vessels, thereby maintaining the concentration of solutes necessary for the operation of such a scheme.   Priestley (1922) believed that an adequate supply of solutes might be provided from the contents of cells which are differentiating into xylem vessels, plus, perhaps, some leakage from the surrounding cells when they are placed under turgor pressure.   As these investigators made most of their analyses on sap from woody species and usually in the spring, they probably overestimated the importance of sugars in maintaining the osmotic pressure of the xylem sap.   According to van Overbeek (1942), no sugar occurs in sap from tomato stumps, except when it is contaminated by phloem exudate, and apparently there is little in the sap of most herbaceous species.   The salt concentration may be relatively high, however.   Eaton (1943) for example, reported osmotic pressures of 1.5 to 2.4 atmospheres in the sap exuding from the stumps of cotton plants, and other data on the composition of xylem sap are given in Chap. 6.

Crafts and Broyer (1938) attempted to explain the accumulation of salts in the xylem by a mechanism which emphasizes the interdependence of root pressure and ion absorption.   Since it is well established that ion absorption and retention by plant tissue are related to metabolism and that, in turn, is related to oxygen supply, poorly aerated cells in the stele are less able to retain a high concentration of solutes than are the well-aerated cells in the outer part of the cortex.   Thus a gradient of salt-absorbing and salt-retaining power exists across the root, the peripheral cells absorbing large quantities of salts from their environment and losing them to the cells that border the stele, which, in turn, lose them to the water in the xylem at the center of the root.   Lundegardh (1940) proposed a somewhat similar explanation of salt accumulation and root pressure, except that he attributed the energy required for salt accumulation to a special type of "anionic respiration."   The necessity of postulating any special type of respiration to account for salt accumulation seems questionable.

Hoagland (1944, pages 84–92) emphasizes the apparently close interrelationship between absorption and accumulation of salts, and the occurrence of root pressure and guttation in barley plants. Root pressure and guttation occur only when the root systems are in well-aerated, dilute salt solutions containing mobile ions, and when they are maintained at a moderate temperature. Guttation becomes negligible or ceases if the roots are immersed in distilled water or unaerated solutions, or if they are kept at low temperatures, all of which conditions are unfavorable to salt accumulation. This view puts primary emphasis on the osmotic movement of water into the root as the cause of root pressure. Such movement would occur whenever the cortical cells of the roots are turgid and when accumulation of salts in the xylem has increased the diffusion-pressure deficit of the xylem sap above that of the external solution. It also stresses as essential to the maintenance of conditions required for continuous inward movement of water the importance of healthy root cells that are well aerated and well supplied with carbohydrates.

Secretory versus Osmotic Theories of Root Pressure. The appearance in recent years of new evidence supporting the occurrence of secretion in living cells has provoked renewed discussion concerning the relative importance of osmotic and nonosmotic forces as causes of root pressure. It has been strongly argued that root pressure can be adequately explained as the result of osmosis alone. Eaton (1943) found that the rate of exudation of cotton root systems was proportional to the difference between the osmotic pressure of the xylem sap and the external solution. Exudation is stopped if the roots are immersed in relatively dilute solutions, and water will be absorbed through the stumps instead of exuding from them. The author (Kramer, 1941) observed that rapid reversal from exudation to absorption and back to exudation by the stump can be observed by transferring detopped root systems from water to dilute

sugar solutions and then back to water. Such reversals require less than a minute and may be repeated many times. This seems to indicate that roots behave as sensitive osmometers. It may be questioned whether a complex secretory mechanism is capable of such rapid and repeated reversal.

The author believes there is sufficient evidence that osmotic movement of water is an important factor in the development of root pressure. Nevertheless, a simple osmotic theory seems inadequate to explain the frequently observed periodicity in rate and magnitude of root pressure or the reaction to auxin and potassium cyanide. There is considerable evidence that the root-pressure mechanism also is related in some manner to the metabolism of the root cells. Went (1944) concluded that the supply of sugar limits exudation from root systems of tomato plants kept in darkness 24 hours prior to detopping. Rate of exudation was increased if one or two leaves were left on the stump and dipped into vials of 1 or 2 per cent sucrose solution. Even if root pressure is largely or entirely an osmotic process, it depends on the existence of differentially permeable membranes in the living cells. The maintenance of this differential permeability depends on energy supplied by respiration; hence, root pressure would be expected to be affected by those factors which affect root metabolism. Furthermore, a relatively high concentration of solutes must be maintained in the xylem sap if osmosis is to occur, and this also requires expenditure of energy by the surrounding living cells. Whether the cells expend energy indirectly in maintaining conditions favorable to osmosis or directly in bringing about the movement of water cannot be decided until we have learned more about the water relations of plant cells.

Passive Absorption by Transpiring Plants

It seems to have been understood, at least in part, by Hales that the forces causing the intake of water by trans-

piring plants are different from those responsible for root pressure. Sachs, Pfeffer, and Strasburger agreed that loss of water by transpiration produces the forces bringing about water absorption by transpiring plants, and that these forces are quite different from those involved in causing root pressure. The gap in their explanation was filled by the discovery of the large cohesive forces of water confined in tubes of small diameter. This fact explains how the forces produced in the shoots by transpiration can be transmitted through the water in the xylem to the roots and can there bring about the intake of water (Dixon, 1914).

As water evaporates from the walls of the mesophyll cells, a diffusion-pressure deficit is produced, which results in the movement of water from the vacuoles, through the cytoplasm, and into the walls. As a consequence of this removal of water, an increase in diffusion-pressure deficit occurs in the cells from which evaporation is taking place and water moves into these cells from adjacent cells, which in turn absorb water from the xylem of the leaf veins. This reduces the pressure on the water in the xylem, and if transpiration is removing water more rapidly than it is being absorbed—as often occurs—tension or negative pressure is developed in the water in the xylem. Subjecting water to tension lowers its diffusion pressure, and this produces a diffusion-pressure deficit numerically equal to the tension applied. Since a more or less continuous liquid system extends through the xylem elements from the leaves to the roots, this deficit is transmitted to the roots. When the diffusion-pressure deficit of the sap in the xylem of the roots is thus lowered below that of the surrounding cells, water begins to diffuse into the xylem. A diffusion-pressure deficit is thus produced in these cells, and a gradient is soon developed across the cortex, along which water moves from the soil to the xylem. If the tension on the xylem sap exceeds the osmotic pressure of the cortical cells, the sap in these cells also is subjected to tension, and water then moves from the soil across the cortex and into the xylem as a continuous, cohesive column. Since

the osmotic pressure of root cells is rather low, and since tensions of several to many atmospheres probably occur in the xylem, it is possible that the root cells frequently are under tension. Under these conditions, movement of water across the cortex might be regarded as mass flow rather than diffusion, since the tension presumably extends to the surface of the peripheral cells of the root.

While the forces that cause the intake of water are under discussion, it may be well to consider the pathway along which water moves from epidermis to xylem. As is indicated in Fig. 14, water must cross 10 to 20 cortical parenchyma cells, the endodermis, and the pericycle before entering the xylem. Presumably, most of the water crosses the protoplast of each of these cells. It is possible that some water movement occurs along the cell walls of the cortical cells, but where the radial walls of the endodermal cells have become suberized, movement can take place only through the protoplasts. Much emphasis has been placed by some workers on the endodermis as the principal differentially permeable membrane in roots. The writer believes, however, that the entire cortex can function as a multicellular membrane, and that the endodermis probably serves no essential function.

Evidently the protoplasm of the living cells offers considerable resistance to the movement of water. The author (Kramer, 1933) found that killing root systems by means of heat or ether resulted in very large increases in the amount of water that moved through them under a given pressure gradient. It would seem, therefore, that water intake might be more rapid through roots having a thin layer of cortical cells than through roots having a thick cortex. The writer believes that the resistance offered to water-movement by the living cells of the root is an important factor in the slowing down of water intake, and that it is frequently the cause of temporary internal water deficits in plants whose roots are adequately supplied with water.

Some discussion has been devoted to the relative impor-

tance of osmotic and imbibitional forces in absorption. Since water moves through cell walls, protoplasm, and vacuoles, and since these are in contact with each other, the imbibitional forces of the walls and the protoplasm must tend to come into equilibrium with the osmotic forces of the vacuolar sap. It is true that, as water evaporates from the cell walls, surface forces are developed in them that cause water to move by what may be termed imbibition from the vacuole into the wall. Discussion of water movement in terms of diffusion-pressure-deficit gradients is more accurate and eliminates any reason for argument concerning the relative importance of imbibitional and osmotic forces. The significant fact is that loss of water from the mesophyll cells of the leaves causes the development of a gradient of diffusion-pressure deficit extending down the stems to the surfaces of the roots and causing water to move from the soil into the roots.

It has been suggested that water movement ought to be discussed in terms of gradients of free energy (Edlefsen, 1941). The free-energy concept has already been mentioned in connection with the movement of soil moisture. Broyer (1947) has published a detailed application of the mathematical treatment used in thermodynamics to water movement and the absorption of solutes in plants, and Edlefsen and Anderson (1943) made a similar application to soil moisture. While such a treatment has advantages for certain purposes, the writer prefers to discuss water movement in terms of diffusion-pressure gradients, because this terminology is just as precise for most purposes and has the further advantage of being intelligible to more people than the thermodynamic treatment would be. The diffusion-pressure deficit of water is a measure of how much lower the free energy of water under a certain set of conditions is than that of the water used as a reference value. The diffusion-pressure-deficit concept can be applied quite precisely to the treatment of plant-and-soil-water relations, and it has the advantage of being more intelligible to most workers in

plant science. For further discussion of the advantages and disadvantages of the thermodynamic treatment, the reader is referred to papers by Edlefsen (1941) and Broyer (1947).

According to the passive theory of absorption, water is absorbed through the roots of plants rather than pumped into the plant by them. In other words, the root systems act as absorbing surfaces, through which water enters the plant because of an energy gradient developed in the shoots. The passive role of the roots is indicated by the fact that plants with dead roots will continue to absorb water from soil at or above field capacity until the roots disintegrate. The water intake through a detopped root system can be materially increased by attaching a vacuum pump to the stump; and even more water will enter through a root system that is subjected to a given pressure gradient after it has been killed than would enter if the same pressure gradient had been applied while it was still alive (Kramer, 1933). According to some observations, more water is absorbed by transpiring shoots after the roots are removed than can be absorbed while they are attached, if care is taken to prevent air from blocking the xylem in the stem (Kramer, 1938). This increase, of course, results from removal of the resistance to water movement offered by the protoplasm in the cortical cells of the roots.

This view of the role of roots in absorption in no way decreases the need for healthy, rapidly growing root systems. As was indicated earlier in this book, only by continuous extension of the roots can adequate contact be maintained with the soil for absorbing the necessary quantities of water and minerals.

Relative Importance of Active and Passive Absorption

For many years there has been discussion concerning the relative importance of active and passive absorption. The evidence available leads the writer to conclude that active absorption, as manifested by root pressure and exudation phenomena, is of negligible importance to plants. Some

of the reasons for this view are as follows: (1) The volume of exudate from stumps is never more than a small percentage of the volume of water lost in transpiration by the intact
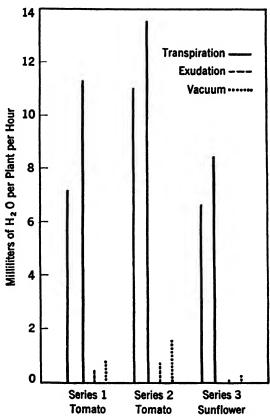
Fɪɢ. 25. Comparison of the rates of transpiration, exudation from detopped plants, and water movement through root systems attached to a vacuum pump. The root systems were in soil at field capacity. (*From Kramer, 1939.*)

plant (see Figs. 25 and 26); (2) intact plants can absorb water from more concentrated solutions and from drier soils than can detopped root systems; (3) no root pressure can be demonstrated in the roots of freely transpiring plants; (4) there is a large group of species, including the gymnosperms, in which root pressure has rarely or never been observed.

In view of the importance of the question, the evidence for these conclusions will be presented in some detail.

Sachs (1882) observed that a leafy shoot of tobacco absorbed 200 ml. of water during the same period of time in
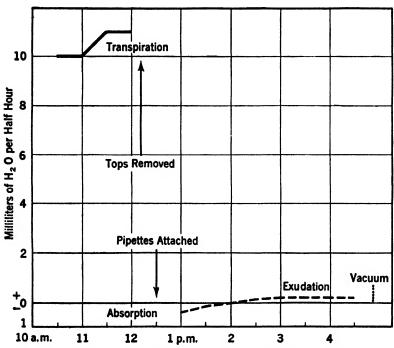
FIG. 26. Behavior of transpiring tomato plants following removal of tops. The roots absorbed water through their stumps for over an hour after removal of the tops. The rate of water movement through the same root systems attached to a vacuum pump was 3.5 times the rate of exudation. Plants were in soil at field capacity. (*From Kramer, 1939.*)

which the stump from which it had been cut exuded only 15 ml. The writer (Kramer, 1939) compared the rates of transpiration of potted coleus, hibiscus, balsam, sunflower, and tomato plants with the rates of exudation from the stumps of the same or similar plants, following removal of the shoots. The rate of exudation usually was only 1 or 2 per cent of the rate of transpiration and never exceeded 5 per cent. Some of the data are shown in Table 5 and in

Table 5. A Comparison of Transpiration and Exudation with the Rate of Transpiration Prior to Removal of the Tops *

(Rapidly transpiring plants usually show absorption during at least the first half hour after the tops are removed, exudation beginning only after the water deficit in the root system is liquidated.)

Species	Number of plants	Transpiration, milliliters of water per plant per hour		Exudation, milliliters of water per plant per hour		Exudation as per cent of transpiration ‡
		First hour	Second hour	First hour	Second hour	
Coleus.....	6	8.6	8.7	0.30	0.28	3.2
Hibiscus...	5	5.8	6.7	−0.01 †	0.05	0.7
Impatiens..	6	2.1	1.9	−0.22	−0.06	
Helianthus	8	4.3	5.0	0.02	0.02	0.4
Tomato (1)	6	10.0	11.0	−0.62	0.07	0.6
Tomato (2)	6	7.5	8.7	0.14	0.27	3.1

↑
Tops removed

* From Kramer (1939).

† A minus sign indicates absorption of water by the stump, instead of exudation.

‡ Percentage relations are based on transpiration and exudation rates for the second hour.

Fig. 25. It is obvious from these data that the root-pressure mechanism could have supplied only a negligible fraction of the water required by the transpiring shoots.

The claim is sometimes made that, although active absorption may not be quantitatively important, it at least supplements passive absorption. Probably, however, no active absorption occurs in the roots of freely transpiring plants. It has been observed ever since the time of Hales that, when cuts are made in the stems of transpiring plants, liquid is at first absorbed through the cut surfaces and, if exudation occurs at all, it begins only after some time has passed. This is illustrated by the data in Table 5 and in

Fig. 26. Furthermore, if the roots are in soil drier than about halfway between field capacity and the permanent-wilting percentage, no exudation ever occurs unless the soil is wetted (Kramer, 1941).

Certain workers have argued that the absence of root pressure following removal of the tops is not adequate evidence that it did not exist in the intact, transpiring plant. Köhnlein (1930) and Romell (1918) suggested that the tension resulting from transpiration stimulates the root cells, causing increased active absorption. It seems highly improbable, however, that if active absorption had been occurring in the transpiring plant it would cease as soon as the tops were removed and would be resumed only after a considerable interval or after the soil is watered. Cessation of exudation certainly is not the result of shock from wounding, because plants which have been in a humid atmosphere show exudation as soon as the tops have been removed. Evidently the cells in the roots of transpiring plants are not, as a rule, fully turgid, and water is absorbed through the stumps until the cells regain completely their turgidity. It seems likely that only after they have become fully turgid can the active absorption mechanism cause water movement into the xylem and the development of root pressure.

There is no direct way of measuring the pressure in the xylem of the roots of transpiring plants except by attaching gauges. This can be done only on large, woody roots. Such measurements as are available indicate the existence of sub-atmospheric pressures in transpiring woody plants. When transpiring herbaceous plants are cut under dye, the xylem is usually stained far down into the roots, as well as up the stems, and this indicates that reduced pressure existed in the roots as well as in the stems. Boonstra (1935) attempted to investigate this problem by sealing roots into potometers in such a manner than any change in volume when the roots were severed from the stem could be measured. In every experiment, a sudden increase in absorption occurred immediately after the roots were cut off from the tops. This indi-

cated that the pressure in the xylem of the roots must have been below rather than above atmospheric pressure, or no absorption could have occurred.

Another method of evaluating the relative importance of forces developed in the roots and in the shoots is by comparing the behavior of intact plants with that of root systems from which the tops have been removed. Renner (1929) found that, although intact transpiring plants of Helianthus developed absorbing forces estimated at 4.1 to 11.7 atmospheres, detopped root systems developed forces of only 1.6 to 2.2 atmospheres.

Tagawa (1934) noted that intact bean plants could absorb water from solutions having osmotic pressures up to 14.6 atmospheres, while the root systems alone could absorb water from solutions having osmotic pressures no greater than 1.9 atmospheres. Plants growing in soil can absorb water in sufficient quantities for growth until the diffusion-pressure deficit in the soil reaches a value of about 15 atmospheres, when absorption becomes so slow that permanent wilting occurs. Root systems from which the tops have been removed can absorb against a diffusion-pressure deficit of only 1 or 2 atmospheres. As a result of this difference, about half of the soil moisture which is available to an intact plant is unavailable to the root system alone.

Renner estimated that transpiring sunflower plants growing in well-watered soil absorb water with a force of 4 to 11 atmospheres, while Köhnlein estimated that a force of 20 to 73 atmospheres would be needed to bring about absorption of the volume of water required by a transpiring sunflower plant. These volumes were determined by measuring transpiration, then detopping the plant and measuring the volume of water obtained by applying a given pressure differential to the stump. From these data it is possible to calculate the pressure required to supply the transpiring shoot. The method can be illustrated by some data presented in Fig. 26. Certain tomato plants observed by the author (Kramer, 1939) had an average transpiration rate of 20 ml.

Fig. 26. Furthermore, if the roots are in soil drier than about halfway between field capacity and the permanent-wilting percentage, no exudation ever occurs unless the soil is wetted (Kramer, 1941).

Certain workers have argued that the absence of root pressure following removal of the tops is not adequate evidence that it did not exist in the intact, transpiring plant. Köhnlein (1930) and Romell (1918) suggested that the tension resulting from transpiration stimulates the root cells, causing increased active absorption. It seems highly improbable, however, that if active absorption had been occurring in the transpiring plant it would cease as soon as the tops were removed and would be resumed only after a considerable interval or after the soil is watered. Cessation of exudation certainly is not the result of shock from wounding, because plants which have been in a humid atmosphere show exudation as soon as the tops have been removed. Evidently the cells in the roots of transpiring plants are not, as a rule, fully turgid, and water is absorbed through the stumps until the cells regain completely their turgidity. It seems likely that only after they have become fully turgid can the active absorption mechanism cause water movement into the xylem and the development of root pressure.

There is no direct way of measuring the pressure in the xylem of the roots of transpiring plants except by attaching gauges. This can be done only on large, woody roots. Such measurements as are available indicate the existence of sub-atmospheric pressures in transpiring woody plants. When transpiring herbaceous plants are cut under dye, the xylem is usually stained far down into the roots, as well as up the stems, and this indicates that reduced pressure existed in the roots as well as in the stems. Boonstra (1935) attempted to investigate this problem by sealing roots into potometers in such a manner than any change in volume when the roots were severed from the stem could be measured. In every experiment, a sudden increase in absorption occurred immediately after the roots were cut off from the tops. This indi-

cated that the pressure in the xylem of the roots must have been below rather than above atmospheric pressure, or no absorption could have occurred.

Another method of evaluating the relative importance of forces developed in the roots and in the shoots is by comparing the behavior of intact plants with that of root systems from which the tops have been removed. Renner (1929) found that, although intact transpiring plants of Helianthus developed absorbing forces estimated at 4.1 to 11.7 atmospheres, detopped root systems developed forces of only 1.6 to 2.2 atmospheres.

Tagawa (1934) noted that intact bean plants could absorb water from solutions having osmotic pressures up to 14.6 atmospheres, while the root systems alone could absorb water from solutions having osmotic pressures no greater than 1.9 atmospheres. Plants growing in soil can absorb water in sufficient quantities for growth until the diffusion-pressure deficit in the soil reaches a value of about 15 atmospheres, when absorption becomes so slow that permanent wilting occurs. Root systems from which the tops have been removed can absorb against a diffusion-pressure deficit of only 1 or 2 atmospheres. As a result of this difference, about half of the soil moisture which is available to an intact plant is unavailable to the root system alone.

Renner estimated that transpiring sunflower plants growing in well-watered soil absorb water with a force of 4 to 11 atmospheres, while Köhnlein estimated that a force of 20 to 73 atmospheres would be needed to bring about absorption of the volume of water required by a transpiring sunflower plant. These volumes were determined by measuring transpiration, then detopping the plant and measuring the volume of water obtained by applying a given pressure differential to the stump. From these data it is possible to calculate the pressure required to supply the transpiring shoot. The method can be illustrated by some data presented in Fig. 26. Certain tomato plants observed by the author (Kramer, 1939) had an average transpiration rate of 20 ml.

per hour per plant. When a vacuum pump was attached to the stumps of these plants, an average of only 0.6 ml. per hour was obtained under a pressure differential of 64 cm. of mercury. From these values it was calculated that a tension, or diffusion-pressure deficit, of 28 atmospheres would be required to bring about absorption of enough water to replace that lost in transpiration. These values are probably too large, because they fail to take into account the fact that, as the tension in the xylem increases, the area of root surface through which absorption occurs also increases. Increased steepness of the diffusion pressure gradient from soil to root undoubtedly causes water to enter through portions of the root surface that are relatively impermeable when a low gradient exists.

In some respects the most significant reason for doubting that active absorption plays an essential part in the absorption of water is the fact that it has seldom or never been observed in the gymnosperms. It would be very surprising to find a process of this nature that would be essential to plants in one division of the plant kingdom, while not even occurring in the plants of another division. White (1942) suggests that, although root pressure is not quantitatively important in transpiring plants, it probably has importance, because it is capable of moving small volumes of water at times when little or no transpiration is occurring. The claim is made, also, that root pressure may be of importance in trees for refilling during the winter those xylem elements which were blocked with air bubbles during the summer. While this may be the case in some species, conifers, which include some of our tallest trees, thrive without that aid. It seems probable that root pressure is the fortuitous result of the root structure and the manner of accumulation of solutes in the xylem of certain species and that those plants exhibiting it would succeed just as well in its absence.

Conclusion

Another way of stating the problem discussed in this chapter is as follows. To what extent is the intake of water by a transpiring plant a function of the entire plant and to what extent is it a special function of the living cells of the root?

The intake of inorganic nutrients, as will be seen in Chap. 10, is clearly a function of the living root cells and is closely related to their metabolic activity. It is not yet known whether or not plant cells can "secrete" or accumulate water as they can accumulate solutes from a surrounding medium, but it is certain that the occurrence of root pressure depends on the existence of healthy, metabolically active cells in the root. Further research will be necessary to discover whether the root cells "secrete" water into the xylem or whether they simply provide a multicellular, differentially permeable membrane across which water moves by osmosis. It seems certain, however, that when transpiration is rapid the active absorption mechanism responsible for root pressure is not only inadequate to supply the required amount of water but actually becomes inoperative, because of the increasing diffusion-pressure deficit in the root cells. Under these conditions, the intake of water is not a special function of the root cells but is a function of the entire plant, the root cells merely providing an absorbing surface, through which water is absorbed. To put it another way, in freely transpiring plants water is absorbed through the roots, rather than by the roots.

CHAPTER 9

FACTORS AFFECTING THE ABSORPTION OF WATER

The rate of absorption of water is determined by a number of factors, which can be classified most conveniently for discussion as plant factors and environmental factors. The plant factors include the extent and efficiency of the root system, the rate of transpiration, and the diffusion-pressure deficit in the water-conducting system. Environmental factors affecting absorption include the available moisture content of the soil, soil aeration and temperature, and the concentration and composition of the soil solution. The environmental factors will be discussed first, and the plant factors will then be considered.

Environmental Factors Affecting Absorption

The variations in soil-moisture content, aeration, and temperature which occur from day to day and from season to season significantly affect the absorption of water, both directly and indirectly. The concentration of the soil solution is high enough in some semiarid and irrigated regions to affect absorption, but it usually is not important in humid regions. The effects of these factors on root growth were considered in Chap. 6, so attention will now be given to their direct effects on water intake. Since water absorption seems to be brought about by two different mechanisms, the effects on both mechanisms will be considered where they appear to differ. Reasons for distinguishing between these two types of absorption have been discussed in Chap. 8.

Moisture Content of the Soil

The relation between the moisture content of the soil and the availability of soil moisture for plant growth was discussed in Chap. 3. This material will be reviewed and some additional information will be presented.

The water readily available for plant growth occurs in the range of soil moisture between field capacity and the permanent-wilting percentage. If the water content is higher than field capacity, air is displaced from the noncapillary pores and absorption is hindered by poor aeration; and if the moisture content is too low, water is held so firmly by the soil that it cannot move into plant roots.

The availability of soil moisture depends primarily on its tension (determined by gravitational, hydrostatic, and surface forces) and its osmotic pressure (determined by the concentration of solutes in the soil solution), both groups of forces tending to decrease its free energy and its diffusion pressure. Free water with a tension and an osmotic pressure of zero is taken as the reference point. The tension on soil moisture at field capacity is about $\frac{1}{3}$ to $\frac{1}{10}$ atmosphere and, as the moisture content decreases, the tension increases—at first slowly and later rapidly—until in the neighborhood of 15 atmospheres of tension permanent wilting occurs. As the tension increases, the gradient of diffusion pressure from soil to root decreases, and this results in slower movement of water from soil to root. Even at a tension, or diffusion-pressure deficit, of 15 atmospheres, slow movement of water from soil to roots occurs; but slight further decrease in soil moisture causes so great an increase in tension and diffusion-pressure deficit of the soil that absorption ceases.

The relation between moisture content and moisture tension is shown in Fig. 3. In the Panoche loam soil, over half of the readily available water is held with a tension of less than 1 atmosphere and nearly 90 per cent, with a tension of less than 5 atmospheres. Reduction in soil-moisture content from 10 to 8.5 per cent triples the tension, and even slight

further reduction causes so enormous an increase in the force with which water is held that movement from soil to roots becomes impossible. In the Chino silty clay loam, less than half of the readily available water is held with a tension of less than 1 atmosphere, and only about 75 per cent is held with a tension of less than 5 atmospheres.

The difference in the curves for these two soils probably explains why some disagreement has arisen as to whether or not water is equally available to plants over the entire range, from field capacity to permanent-wilting percentage. In fairly coarse-textured soils, such as the Panoche loam, where most of the water in this range is held with a tension of less than 1 atmosphere, practically all of it is equally available. In fine-textured soils, such as the Chino, where less than half of the available water is held with a force of less than 1 atmosphere, a considerable part of the water in the lower part of the range is less available than that in the upper part. As the soil-moisture content approaches the permanent-wilting percentage, a small decrease in moisture content is accompanied by a very large increase in tension and diffusion-pressure deficit. The diffusion-pressure deficit of the soil, therefore, soon exceeds any possible diffusion pressure deficit that can be developed in a plant, and absorption ceases.

McDermott (1945) studied the effect of soil-moisture content on exudation from detopped sunflowers growing in soil. He found that no exudation occurred from root systems in soils with moisture contents in the lower 60 per cent of the range of readily available moisture. Furthermore, exudation was reduced by high soil-moisture content, no doubt because of poor aeration. The results of this experiment are shown in Fig. 27. In another series of experiments, the author (Kramer, 1941) found that the limiting moisture content for exudation was about halfway down the range from field capacity to permanent wilting. These data show rather definitely that water is less available in the lower half of the range of readily available moisture than in the upper

half, so far as the active absorption mechanism is concerned.

Available data indicate that soil-moisture content within the range of readily available moisture affects the rate of transpiration. Chung (1935), working with plants that grow in soil with a minimum moisture content well above the permanent-wilting percentage, found that the greater the moisture content of the soil, up to a certain point, the
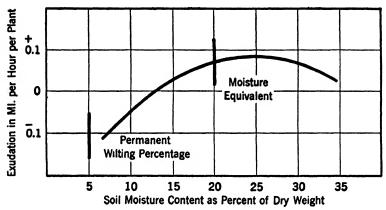
Fig. 27. Relation between rate of exudation from sunflower root systems and moisture content of the soil. Plus values indicate exudation; minus values, absorption of water by the stumps. (*From McDermott, 1945.*)

greater the rate of transpiration. Martin (1940) found the rate of transpiration per unit of leaf surface of sunflower plants ordinarily was reduced when about two-thirds of the readily available water had been absorbed from the soil in which the plants were growing. The reduction in transpiration was accompanied by closure of stomates and some loss of turgidity, no doubt because absorption lagged too far behind transpiration. It thus appears that the soil moisture in the lower part of the range of readily available water is somewhat less available to the passive absorption mechanism of transpiring plants, just as it is to the active absorption mechanism of detopped root systems.

In Chap. 2, data were presented supporting the view that growth is sometimes checked at soil-moisture contents above

the permanent-wilting percentage. That this may depend on weather conditions is indicated by the fact that Magness, Degman, and Furr (1935) found that, when transpiration was rapid, growth rate of apples and period of stomatal opening were reduced if the moisture content of any considerable portion of the soil in the root zone was reduced to the permanent-wilting percentage. If, on the other hand, the weather was cool and moist, fruit growth was almost normal, even though the soil moisture in the entire root zone was approaching the permanent-wilting percentage. Martin (1940) reported that growth of sunflowers was reduced by small decreases in soil-moisture content, even though the moisture content was well above the permanent-wilting percentage. According to Scofield (1945a), alfalfa grown with a continuous water supply provided by subirrigation yielded more hay than alfalfa watered intermittently, although the latter was never allowed to reduce the soil moisture to the permanent-wilting percentage. Wadleigh and Gauch (1948) found no reduction in elongation of leaves on cotton plants subjected to a moisture stress of 1 to 3 atmospheres, but elongation was reduced by a stress of 10 to 12 atmospheres and ceased at 15 atmospheres.

The moisture content of the soil mass occupied by a given root system is not necessarily reduced uniformly. The soil in contact with the roots presumably is dried to the permanent-wilting percentage, while that at a distance of a few millimeters is often still at or near field capacity. The moisture content of a soil sample is, therefore, simply the average moisture content of the soil between the roots and that in contact with them. The region nearest the plant usually is dried out first because it is first occupied by roots; and if no water is added, the zone of dry soil gradually extends deeper and farther outward from the plant as the root system extends (see Figs. 28 and 29). It is well established that the extent to which moisture is removed from the soil depends largely on the concentration of roots in the soil (Aldrich, Work, and Lewis, 1935: Veihmeyer and Hendrickson,

1938*b*). It has been claimed that moisture at a distance from the plant is less available than that near by, even when both regions are occupied by roots. Davis (1940) observed that roots of corn plants continued to absorb water near the plant from soil at or near the wilting percentage, while roots
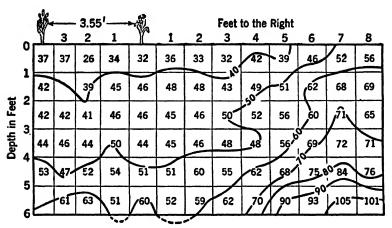
Fig. 28. Reduction in moisture content of soil on which a crop of sorghum was grown. Moisture was reduced approximately to the permanent-wilting percentage to a distance of 6 ft. beyond the outside row and to a depth of about 5 ft. The irregular lines join points of equal relative wetness (see Chap. 2 for definition of relative wetness). A relative wetness of 50 per cent is approximately equal to the permanent-wilting percentage of this soil. (*From Conrad and Veihmeyer, 1929.*)

2 to 4 ft. away were in soil well above the permanent-wilting percentage. When the roots near the plant had reduced the moisture content of the soil to the permanent-wilting percentage, the roots 3 or 4 ft. away in soil well above the wilting percentage were unable to prevent wilting. This led Davis to suggest that distance from the plant might be a factor in the wilting percentage and that determinations made with small plants in pots might, therefore, be somewhat different from those determined with large plants of the same species in large volumes of soil.

It seems more likely that the differences are the result of differences in amount and concentration of roots rather than

of any real decrease in absorbing power at a distance from the plant. Such a decrease could be caused only by friction or resistance to water movement through the root, a factor which probably amounts to less than 1 atmosphere in the distances involved. The distance factor apparently is not
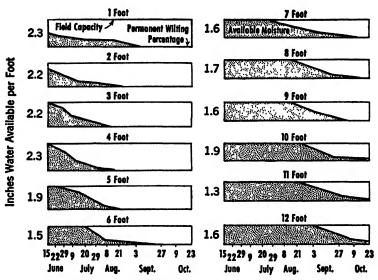
Fig. 29. Rate of water extraction from various depths in an unirrigated soil by tomato plants. Water was progressively extracted from the deeper levels as the roots penetrated into them. Growth slowed down by early August, when most of the readily available water had been removed from the upper 6 ft. of soil. A total of 21 in. of water was removed by Oct. 23. This plot yielded only half as well as an irrigated plot. (*From Doneen and MacGillivray, 1946.*)

too serious, because Reimann, van Doren, and Stauffer (1946) found corn thriving, although by early August it had exhausted all available water in the upper 3.5 ft. of soil and was absorbing its water from a depth of 3.5 to 6.5 ft. Veihmeyer and Hendrickson (1938b) found that water 20 ft. from a tree is absorbed just as readily as that which is only 6 or 8 ft. distant.

Only a part of the root system need be in soil above the permanent-wilting percentage to provide water for limited

growth and survival. Taylor, Blaney, and McLaughlin (1934) concluded that plants can absorb enough water to replace transpirational losses if one-fourth to one-half of their root system is in soil above the permanent-wilting percentage. Furr and Taylor (1939) found that, where lemons grow on a shallow soil underlain by a dense subsoil, enough water can be absorbed from the subsoil to prevent wilting and to maintain slow growth for some time after the readily available water is removed from the surface soil. To maintain good growth, however, the surface soil where most of the roots are concentrated must be kept above the permanent-wilting percentage. They found that if all the soil in one-half of the root zone was kept above the permanent-wilting percentage, this sufficed to prevent development of any serious water deficit in the tree. This is in accord with the view previously expressed that most plants have root systems considerably larger than would be necessary for providing them with water.

There is some difference of opinion concerning the extent to which roots can reduce soil moisture below the permanent-wilting percentage. Batchelor and Reed (1923) reported that in certain Persian-walnut groves (*Juglans regia*) the soil was reduced to the wilting point by mid-June and that by the end of October the upper 7 ft. of soil were down to the hygroscopic coefficient; yet the trees survived. Similar conditions were believed to exist in most fruit orchards in that region. On the other hand, Taylor, Blaney, and McLaughlin state that they have never found soil-moisture contents lower than the ultimate wilting point in soil samples taken below the depth affected by surface evaporation. They found that native vegetation reduced the region of maximum root concentration to the ultimate wilting percentage; then, as an increasing proportion of the soil occupied by their roots is depleted of available water, they become more or less dormant and survive on the limited amount of water absorbed by a few deep roots in soil still containing available water. This probably is what occurs

in most plants during droughts. During later summer droughts, most of the root system of dogwood and other shallow-rooted understory vegetation of Eastern forests frequently must be in soil dried to the permanent-wilting percentage.

Aeration

According to Clements (1921), who summarized the early literature on aeration, De Saussure made one of the earliest investigations of the effects of inadequate aeration on absorption. He observed that pea plants wilted when pure carbon dioxide or mixtures containing two-thirds or three-fourths carbon dioxide were passed through the nutrient solution in which they were growing. Numerous other observations were made during the nineteenth century, including work by Barthelemy, Burgerstein, Kosaroff, Kossevitch, and Wolf. Kossevitch (1892) observed that an atmosphere consisting of 80 per cent carbon dioxide and 20 per cent oxygen caused peas that were growing in soil to wilt within 2 days. A mixture of 80 per cent hydrogen and 20 per cent oxygen caused no wilting, and this indicates that carbon dioxide exerted a specific effect. Kosaroff (1897) found that both absorption and transpiration of rooted plants in potometers were reduced when carbon dioxide was passed through the water in the potometers. Since these processes were retarded much less by hydrogen, Kosaroff concluded that any effects from hydrogen were the result of displacement of oxygen, and that carbon dioxide itself retards absorption.

Livingston and Free (1917) observed that *Coleus blumei* and *Heliotropium peruvianum*, growing in autoirrigated containers, ceased to absorb water within 12 to 15 hours after the soil atmosphere was replaced by nitrogen, and that they soon wilted and died. Absorption of water by *Salix nigra* was not affected by nitrogen, the roots of this plant apparently growing and absorbing in almost complete absence of oxygen. Bergman (1920) reported that plants of Phaseolus, Impatiens, and Pelargonium, growing in soil,

wilted badly within 2 days after the pots were immersed in water. When the air surrounding pots containing Pelargonium and Impatiens was replaced by carbon dioxide, the plants wilted in 2 or 3 days. Hunter and Rich (1925) found that aeration of the soil in which *I. balsamina* was growing caused increased transpiration. Arnon and Hoagland (1940) observed that tomatoes growing in unaerated culture solutions frequently wilted on warm, sunny days, but recovered when air was bubbled through the tanks. No wilting was observed in aerated tanks. These investigators concluded that, in general, the oxygen supply of unaerated solution cultures is inadequate for maximum growth. Accumulation of carbon dioxide might also be a factor, because aeration removes carbon dioxide at the same time that it supplies oxygen. Childers and White (1942) found that submergence of roots of young apple trees caused reduction in rate of growth of tip leaves within a week. Transpiration and apparent photosynthesis also were reduced usually within a week, but sometimes transpiration was not much reduced until after 3 or 4 weeks. These observations are, of course, merely quantitative and controlled demonstrations of what is frequently observed when roots of plants are poorly aerated under field conditions.

Poor aeration retards not only root growth and water absorption, but also the absorption of minerals. Arnon and Hoagland found that tomato plants growing in aerated solutions absorbed larger quantities of all nutrients and produced larger yields of fruit than did plants growing in unaerated solutions. They concluded that aeration may be inadequate for maximum absorption of nutrients by at least some species in the average cultivated soil. Not all species require as good aeration as do tomatoes, for Vlamis and Davis (1944) reported that intact rice plants will absorb adequate amounts of water and nutrients, even when the roots are under anaerobic conditions. Chang and Loomis (1945) found that absorption of nutrients by corn and wheat

was greatly reduced by bubbling carbon dioxide through the nutrient solutions, but not by introducing nitrogen.

How Inadequate Aeration Reduces Absorption. Although it has been well established that poor aeration reduces absorption of water and minerals, the causes of the reduction are not so well understood. The reduction might be caused by reduced metabolic activity of the roots, by physical changes in permeability, or by a combination of the two. Livingston and Free (1917) suggested that coagulation of protoplasm in the roots, accompanying their death, might suffice to explain the reduced water intake on a purely physical basis. Hunter and Rich (1925) also suggested that poor aeration causes decreased permeability of the roots to water. The author (Kramer, 1940*b*) found that saturating the soil or the water in which sunflower and tomato plants were growing with carbon dioxide reduced transpiration 34 to 52 per cent, exudation 63 to 74 per cent, and exudation from root systems attached to a vacuum pump 35 to 65 per cent. Saturating the water in which root systems were immersed with nitrogen reduced transpiration and exudation less than 10 per cent. Bubbling air through the water in which detopped root systems were immersed had no effect on exudation during the first hour, but increased it about 30 per cent the second hour. These results indicate that absorption is reduced more by excess of carbon dioxide than by deficiency of oxygen, at least during the first few hours (see Fig. 30).

Chang and Loomis (1945) reported that absorption of water by root systems of corn, wheat, and rice, growing in culture solutions, was reduced 14 to 50 per cent by bubbling carbon dioxide through the solutions 10 minutes out of every hour. Rice was apparently more affected by carbon dioxide than were the other species studied, but this may be because the experiments with rice were conducted at higher temperatures than those with wheat and corn. Both air and nitrogen bubbled through the cultures produced small increases in absorption of water, possibly because they prevented accumulation of carbon dioxide. These experiments showed

that carbon dioxide definitely reduced the permeability of roots to both water and solutes. Hoagland and Broyer (1942) attached stumps of tomato-root systems to a vacuum
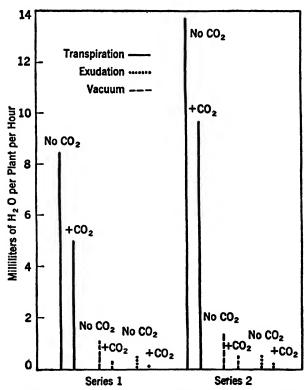
FIG. 30. Effects of carbon dioxide on water movement through tomato root systems. While the percentage reduction in exudation is much greater than the percentage reduction in transpiration, complete cessation of exudation would account for less than 15 per cent of the reduction in transpiration. (*From Kramer, 1940b.*)

line and measured the rate of exudation with the roots in a well-aerated solution. When the solution surrounding the roots was saturated with carbon dioxide, exudation was quickly reduced to only 15 per cent of the original rate, but after about 6 hours it began to increase and after 24 hours it was 1.8 times the original rate. The increased water

movement probably resulted from increased permeability, accompanying injury to the protoplasm from prolonged exposure to carbon dioxide.   Saturation of the solution sur-
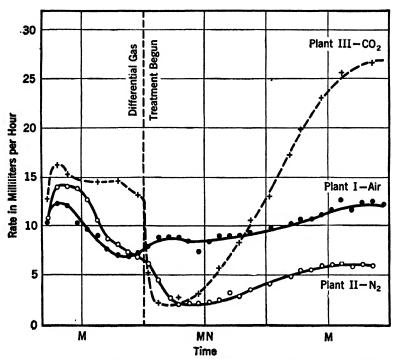
FIG. 31. Effects of nitrogen and carbon dioxide on water movement through tomato root systems attached to a vacuum pump. Air was passed through the solution surrounding the roots of plant I, nitrogen plant II, and carbon dioxide plant III. Both nitrogen and carbon dioxide caused an initial decrease in rate of water movement, probably because of decreased permeability. This was followed by a large increase from the root system treated with carbon dioxide, suggesting increased permeability as the result of injury to the roots. (*From Hoagland and Broyer, 1942.*)

rounding the roots with nitrogen depressed the rate of exudation, which did not rise to the original rate, even after 24 hours.   This seems to constitute further evidence that exposure to carbon dioxide will produce changes in metabolic activity and in permeability sooner than deficiency of oxygen will.   The results of this experiment are shown in Fig. 31.

There is some evidence that over longer periods of time oxygen deficiency may have more effect than an excess of carbon dioxide has. Whitney (1942) grew plants of coleus, corn, cotton, sunflower, tobacco, and tomato in sand-filled containers arranged so they could be aerated with various gas mixtures. The root systems were aerated at a rate of 2 liters per hour for 7 to 14 days. The mixtures used were air; 20 per cent carbon dioxide, plus 20 per cent oxygen, plus 60 per cent nitrogen; pure nitrogen; and 20 per cent carbon dioxide, plus 80 per cent nitrogen. Lack of oxygen decreased transpiration of all species and caused death of many roots of coleus, tobacco, and tomato plants. Aeration with 20 per cent carbon dioxide in the presence of 20 per cent oxygen did not reduce transpiration of corn, cotton, or sunflower and but slightly reduced transpiration of coleus, sunflower, and tomato. Aeration with 20 per cent carbon dioxide and 80 per cent nitrogen reduced transpiration of some species little more than oxygen deficiency alone had done; but coleus was killed, and transpiration of tomato was reduced more than by oxygen deficiency or by carbon dioxide plus oxygen. The writer is unable to explain the discrepancy between these results and the others just cited, but it is well to remember that these plants were grown in sand and that the experiments were continued over a considerable period of time. Further investigation of this problem seems desirable.

It is easy to explain the harmful effect of oxygen deficiency on absorption by attributing it to reduction in rate of aerobic respiration and accumulation of incompletely oxidized toxic products of anaerobic respiration. Since permeability is closely related to metabolism, this disturbance of normal metabolism may result in changes in permeability and finally in death of the root cells. It is even possible that toxic substances might be translocated from the roots to other parts of the plant, causing injury. Such changes would presumably require at least several hours—perhaps longer—to take place, whereas the effects of carbon dioxide

are immediate. According to Fox (1933), carbon dioxide has a specific narcotic effect on protoplasm, causing an increase in viscosity of the protoplasm of Nitella. Seifriz (1942) observed that carbon dioxide exerts similar effects on the plasmodium of a certain slime mold. Chang and Loomis suggest that the toxic effects of carbon dioxide may be related to its ability to change the internal pH of cells and to form hydrogen-bond compounds with proteins, thereby increasing the viscosity of protoplasm and decreasing permeability of protoplasmic membranes. Decreasing the pH of the external solution with strong acid is not so effective as using carbon dioxide, possibly because the latter penetrates cell membranes more rapidly (Jacobs, 1922).

Regardless of the exact mechanism of the action, it has been demonstrated that an excess of carbon dioxide decreases the absorption of water more quickly than does a deficiency of oxygen. This is to be expected, since displacement of oxygen by nitrogen or hydrogen is not instantaneous, and besides it prevents accumulation of carbon dioxide. Possibly some oxygen is available in the tissues and some might diffuse down from the shoots; so oxygen deficiency would not be expected to develop as rapidly as the effects of excess carbon dioxide do. Furthermore, if oxygen deficiency reduces absorption through toxic effects of end products of anaerobic respiration, some time would be required for a sufficient concentration of these to develop. Chang and Loomis believe that slightly toxic concentrations of carbon dioxide may occur more frequently than limiting concentrations of oxygen. McComb and Loomis (1944) suggest that even moderate concentrations of carbon dioxide might affect competition between species by reducing water and mineral absorption of the more sensitive species. If upland forest trees, for example, have roots less tolerant of carbon dioxide than those of grasses and other prairies species, this might help to explain the failure of such trees to invade grasslands, where root respiration and decay of the abundant organic

matter probably create a relatively high concentration of carbon dioxide.

In conclusion, the evidence suggests that the considerable reductions in absorption of water by plants in poorly aerated media are—at least, initially—the result of decreased passive absorption, caused by decreased permeability of the roots to water. While poor aeration decreases or stops the active-absorption mechanism, complete cessation of active absorption would not account for more than a small fraction of the total reduction observed in rapidly transpiring plants and is, therefore, of negligible importance.

Effects of Soil Temperature on Absorption

It has been known, at least since the time of Hales, that low soil temperatures reduce the absorption of water. Sachs observed that tobacco and gourd plants growing in moist soil under conditions favoring a low rate of transpiration wilted when the soil was cooled to 3 to 5°C., but recovered when it was warmed to 12 to 18°C. Cabbage and turnip were less affected, as they absorb enough water at a soil temperature just above freezing to prevent wilting during periods of moderate transpiration. In general, it has been found, as might be expected, that plants which are native to warm climates or which normally grow in warm soil exhibit a greater reduction in water intake than do plants which normally grow in cooler soils and during the cooler seasons. Döring (1935) made an extensive comparison of the behavior of species from different habitats, the results of which indicate that water intake of plants from cold, wet moors was reduced less by cooling the soil than was water intake of plants from warm, dry soils. Brown (1939) found that water absorption by Bermuda grass, a native of warm regions, is sufficiently retarded at 10°C. to cause wilting, although bluegrass, which occurs in cooler sections of the country, is unaffected.

Arndt (1937) reported that cotton plants wilted at soil temperatures of 17 to 20°C. and that plants in solution culture wilted at 10 to 18°C. when first exposed to conditions

favorable to high transpiration.   At soil temperatures lower than about 20°C., cucumber plants do not absorb enough water to replace transpirational losses, hence injury from desiccation may occur.   According to Schroeder (1939), cold soil, aggravated by watering with cold water, often causes serious injury to greenhouse cucumbers.   Raleigh (1941) found that water absorption by muskmelon plants is very slow at 10°C. and is much slower at 18 than at 27°C.   Cotton, cucumbers, and muskmelons thrive only in warm soil.

The rate of absorption of water by various species of plants in cold soil has been studied in the author's laboratory (Kramer, 1942), and the results are summarized in Table 6.

Table 6.   Effects of Soil Temperature on Water Absorption by Plants of Various Species *

(Rates of transpiration were measured and it was assumed that absorption was approximately equal to transpiration over 24-hour periods.)

Experiment	Species	Number of plants per experiment †	Final soil temperature	Transpiration of cooled plants as per cent of controls at 25°C.
1	Collards (*Brassica oleracea acephala*)	6	12.0	63.0
	Cotton (*Gossypium hirsutum*) . . .	6	12.0	7.4
2	Collards	6	4.3	53.0
	Cotton	6	4.3	4.3
3	Collards	6	1.0	33.0
	Watermelon (*Citrullus vulgaris*)	6	1.0	1.4
4	Loblolly pipe (*Pinus taeda*)	4	0.5	13.7
	Slash pine (*P. caribaea*)	4	0.5	13.9
	White pine (*P. strobus*)	4	0.5	37.7
	Red pine (*P. resinosa*)	4	0.5	25.0
5	Elm (*Ulmus americana*)	14	0.5	25.0
6	Privet (*Ligustrum japonicum*) . .	12	2.5	47.0
7	Sunflower (*Helianthus annuus*) .	12	1.0	27.0

* Modified from Kramer (1942).

† The plants were divided into two groups, one of which was cooled about 5°C. per night while the other was kept at 25°C.

It will be observed that absorption by species which grow in the winter, such as collards, and by species native to cooler climates, such as white and red pine, is reduced less by low soil temperatures than is absorption by warm-weather crops, such as cotton and watermelon, and by southern pines, such
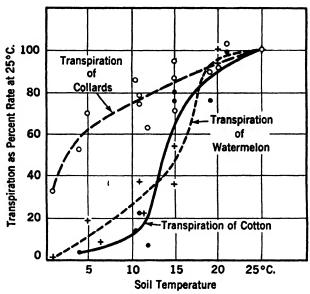
FIG. 32. Effects of soil temperature on water absorption of various species of plants, as measured by rate of transpiration. Collards thrive in cold soil; cotton and watermelons, in warm soil. (*From Kramer, 1942.*)

as slash and loblolly. Privet, an evergreen species, is less affected than is the deciduous elm. Kozlowski (1943) found that absorption by loblolly pine was reduced much more between 15 and 5°C. than was absorption by white pine. Some differences between species are shown graphically in Fig. 32. These data suggest the existence of fundamental differences between species in the reaction of protoplasm to low temperature. Possibly the permeability of the protoplasm of some species is reduced more than that of others. This is in accord with the statement of Levitt and Scarth (1936) that cells of cold-hardened plants are more permeable than are those of plants that are not cold hardened.

Cameron (1941) reported that in California orange trees frequently wilt severely during periods of cold weather. This probably is the result of reduced absorption from cold soil, as research by Cameron, Bialoglowski (1936), and Haas (1936) indicates that cooling the soil materially reduces absorption of water and transpiration by oranges, lemons, and grapefruit. L. H. Jones (1938) discovered that gardenia plants often become chlorotic at soil temperatures lower than 20°C. and that plants moved from high to low temperatures often wilt, although they usually recover eventually. Cold soil may be of some ecological importance. Whitfield (1932) and Clements and Martin (1934) believed that the low soil temperatures occurring at high altitudes may limit plant growth, and Michaelis (1934) suggested that slow absorption in cold soil at high altitude may affect the position of timber lines. It seems probable that considerable winter injury may result from desiccation caused by cold soil's retarding absorption during periods when atmospheric conditions are favorable to transpiration. This may be one reason why evergreen shrubs often survive winter weather better in partial shade than they do in full sun.

High soil temperatures may also limit absorption. Bialoglowski (1936) found that root temperatures of 35°C. or higher reduced absorption of water by lemons, and Haas (1936) reported that absorption by lemons, Valencia oranges, and grapefruit was decreased by soil temperatures higher than 30 or 35°C. Clements and Martin stated that transpiration of water by sunflower was little affected by soil temperature from 12.5 to 37.5°C., but the data graphed in Fig. 2 of their paper shows a maximum at about 24°C. and a decrease at 37.5°C. which probably resulted from decreased absorption at the higher temperature. The writer found that exudation from detopped tomato plants attained a maximum at about 25°C. and decreased as the soil temperature was increased (Kramer, 1940a).

The suddenness and length of exposure to a new temperature may have some influence on the extent to which it

affects the rate of absorption. Barney (1947) found that at low temperatures the rate of absorption by loblolly pine seedlings decreased for a day or two, then increased somewhat. Bialoglowski (1936) noted that absorption of water by rooted lemon cuttings decreased with length of exposure at very high and at very low temperatures, perhaps because of progressive injury to the roots at these extreme temperatures. The writer has observed that some species of plants wilt when their root systems are suddenly cooled, but recover after a time, probably because transpiration is reduced to the point where it no longer exceeds absorption. Bialoglowski observed that night transpiration of lemon cuttings was not affected by low soil temperature, apparently because the night rate was so low that the rate of absorption did not become limiting, even in a soil near freezing. This is an example of a general situation—namely, that the effect of any factor hindering absorption is most noticeable when transpiration is high and least noticeable when it is low. At times of low transpiration, it is difficult to demonstrate wilting caused by cold soil, too-concentrated soil solution, or removal of part of the root system, although such wilting is easily demonstrated when transpiration is rapid.

Causes of Decreased Absorption at Low Temperatures

It is not surprising to find that low soil temperature reduces the absorption of water, for it can act in several ways. The most important are as follows:

1. Retardation of root elongation, which decreases rate of penetration of roots into new regions of the soil. This is of some importance in soils drier than field capacity.

2. Decreased rate of movement of water from soil to roots. The water-supplying power of the soil as measured with soil-point cones is only one-third to one-half as great at freezing as at 25°C.

3. Decreased permeability of cells. In general, permeability of cells to water decreases with decreasing temperature. The temperature coefficient of diffusion through cell

membranes is much higher than for diffusion in aqueous systems, mostly for reasons which are considered in the next two paragraphs.

4. Increased viscosity of protoplasm and of the colloidal gels in the cell walls. In general, the viscosity is several times as great near freezing as at 25°C., and this certainly retards water movement across the mass of cells lying between the epidermis and the xylem of the root.

5. Increased viscosity of water. Its viscosity is twice as great at freezing as at 25°C. It is likely that this slows down not only the movement of water from soil to root, but also its movement through the root.

6. Decreased vapor pressure of water. The vapor pressure of water is only about one-fifth as great at freezing as at 25°C.

7. Decreased metabolic activity of the living tissues of the roots. This is important with respect to the active-absorption mechanism if that process is either directly or indirectly dependent on the expenditure of energy by the tissues of the root. It is important also in passive absorption, because metabolic activity probably affects the permeability of protoplasmic membranes.

It is well known that root-pressure and exudation phenomena do not occur at low temperatures. The writer found that active absorption as measured by exudation from detopped sunflower- and tomato-root systems is most rapid at 25°C., decreasing at higher and at lower temperatures. In some series of experiments, it ceased at 12° in tomatoes and at about 2.5°C. in sunflower (Kramer, 1940a). The effects of temperatures higher than 35°C. were not studied, but the process doubtless ceases at temperatures high enough to cause injury to the protoplasm.

Wilting of plants in cold soil cannot be attributed to decrease in or even complete cessation of active absorption because, as has been previously stated, even under favorable conditions it supplies so small a fraction of the total amount of water required by the shoot. It was found, however, that

water movement through root systems in soil and in water attached to a vacuum pump was less than one-fifth as great at near-freezing temperatures as it was at 25°C. This indicates that there is a high resistance to water movement through roots at low temperatures. When the root systems were killed by immersion in hot water and were then cooled, water movement was about half as rapid at zero as at 25°C. This indicates that much of the resistance is removed by destroying the protoplasm. These results are shown graphically in Fig. 33. Curves for water movement at various temperatures through dead roots and through collodion and porcelain membranes are very similar, suggesting that the rates are controlled primarily by the viscosity and the vapor pressure of the water itself (Kramer, 1940a).

It is concluded that the principal cause of reduced intake of water by transpiring plants in cold soil is the physical effect of increased resistance to water movement across the living cells of the roots. This results from the combined effects of the decreased permeability and increased viscosity of the protoplasm of the living cells in the roots and the increased viscosity and decreased diffusion pressure of the water intake. Other factors, such as decreased root extension, water-supplying power of the soil, and metabolic activity of the roots, are of distinctly secondary importance.

Differences between species in the extent to which absorption is hindered by low temperature may be the result of differences in the degree of change in viscosity and permeability of protoplasm. It is possible, for example, that the protoplasm of cotton or watermelon roots undergoes much greater changes in viscosity and permeability than does the protoplasm of collards, with, as a result, a greater decrease in water absorption by these species at low temperatures. In experiments with elm, privet, and sunflower, it was found that plants which were cooled nearly to freezing in 4 or 5 hours, or even overnight, wilted severely; whereas, plants cooled over a period of 4 or 5 days wilted but slightly. The

rapidly cooled plants also transpired less than did the plants that were slowly cooled to the same temperature.   It seems
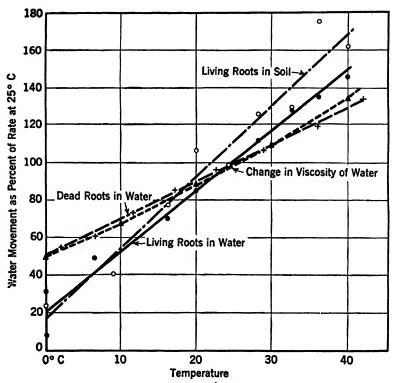
Fig. 33.   Effects of temperature on rate of movement of water through living and dead sunflower roots attached to a vacuum line producing a pressure differential of 64 cm. of mercury.   Living root systems were under vacuum only one hour at each temperature, a new set of plants being used for each test.   To facilitate comparison between dead and living roots, rates are plotted as percentages of the rates at 25°C.   Change in viscosity is expressed as percentages of the reciprocal of the specific viscosity at 25°C. Note that change in temperature affects water movement through living roots more than through dead roots, probably because of the high viscosity of living protoplasm.   (*From Kramer, 1940a.*)

possible that slow cooling affords time for the occurrence of changes in protoplasmic properties that mitigate the effects of cooling on absorption.

Concentration and Composition of the Soil Solution

In humid regions, the osmotic pressure of the soil solution seldom is high enough to limit plant growth; but in arid and irrigated soils, it often becomes a limiting factor. Osmotic pressures of 10 to 200 atmospheres occur in certain soils of the western United States. According to Magistad and Reitemeier (1943), the osmotic pressure of the soil solution from soils suitable for crops ought not exceed 2.0 atmospheres at the permanent-wilting percentage. Growth of crops is definitely limited by osmotic pressures of 2 to 4 atmospheres, while soils having osmotic pressures of about 40 atmospheres or more are barren. In humid regions, addition of fertilizer occasionally results in osmotic pressures too high for the best growth of plants. Application of 1,200 lb. of 3-9-3 fertilizer per acre to Norfolk sandy loam, for instance, increased the osmotic pressure of the soil solution to about 14 atmospheres (White and Ross, 1939). A similar application to Cecil clay loam produced an osmotic pressure of only 3 atmospheres. Excessively high concentrations of salts also occur occasionally in greenhouse soils, causing serious reduction in growth.

Both concentration and composition of the soil solution affect the absorption of water, but the effects of differences in composition appear to be largely indirect. Thus the presence of large quantities of sodium and potassium in the soil produces alkali soils, which are characterized by puddling, impermeability, waterlogging, and poor aeration—all of which are, either directly or indirectly, unfavorable to absorption. Saline soils contain an excess of salts, but not an excess of sodium and potassium in the exchange complex. In such soils, total concentration of salt seems to be more important than relative concentration of various ions. Although chlorides are generally believed to inhibit growth more than sulfates do, the differences are not great in solutions of equal osmotic pressure.

Early investigations of the effects of salts on plant growth

were concerned with the relative effects of various ions and proportions of ions in terms of antagonism, physiological balance, toxicity, and effects on permeability. The results were contradictory, confusing, and unsatisfactory. At present there is a tendency to emphasize the osmotic, or physical, effects of total concentration on the moisture stress in plants, rather than the chemical effects of individual ions on permeability, etc. Eaton (1942) pointed out that general observations as well as specific experiments show no evidence of the existence of a critical concentration above which symptoms of injury appear. Instead, above a rather low concentration, each increase in concentration produces a further but lesser decrease in growth. In the lower concentrations where this effect begins to appear, it is almost imperceptible unless actual measurements of growth are made. Magistad *et al.* (1943) found a practically linear relationship between osmotic pressure of the soil solution and growth of a dozen different species of crop plants over the range from 0.4 to 4.5 atmospheres. Reduction in growth with osmotic pressure of the soil or the culture solution has been reported by a number of other investigators, including Ayers, Wadleigh, and Magistad (1943), Hayward and Long (1943), Wadleigh and Ayers (1945), and Wadleigh, Gauch, and Magistad (1946). The work of these investigators indicates that quite similar reductions in growth occur in plants subjected to similar moisture stress, whether this stress is produced by growing the plants in dry soil or by growing them in salt solutions (see Figs. 34 and 35). It appears, therefore, that the major cause of decreased growth in saline soils is decreased availability of water rather than any specific toxic effects of the salts. Although specific ionic effects exists, they appear to be secondary to the reduction in absorption of water.

Experiments on entire root systems and on single roots show that absorption of water is materially affected by the osmotic pressure of the solution surrounding the roots. Rosene (1941a) found that water intake by detached roots

of *Allium cepa* was stopped by solutions having an osmotic pressure of 1.8 to 3.3 atmospheres, whereas absorption by attached roots was stopped by solutions having osmotic pressure of 4.2 to 5.7 atmospheres. Sucrose and potassium
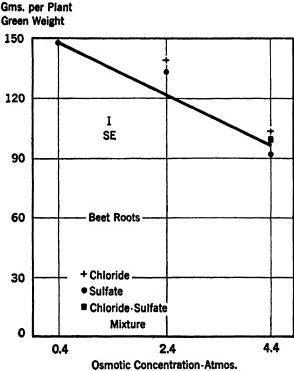
Fɪɢ. 34. Yield of garden beets grown in culture solutions of various concentrations and compositions. Chlorides and sulfates reduced yields to the same extent. (*From Magistad, et al., 1943.*)

nitrate were equally effective in reducing absorption. Hayward and Spurr (1943, 1944) obtained similar results with corn roots. Water intake from a salt solution having an osmotic pressure of 4.8 atmospheres was only 12 per cent of the intake from a nutrient solution having an osmotic pressure of 0.8 atmosphere. Solutions of sucrose, mannitol, sodium sulfate, sodium chloride, and calcium chloride of the same osmotic pressure reduced water absorption to the

same extent. These results support the view of Meyer (1931) and other workers that, with respect to reduction in water intake, total concentration of solutes is more important than the kind of solute. The possibility of specific ionic effects should not be ignored completely, however.

The effect of osmotic pressure of the substrate on water absorption has been demonstrated also by a split-root technique. Eaton (1941) grew corn and tomato plants with their root systems divided between solutions of different composition and osmotic pressure. Root growth and volume of water absorbed were always greater in the dilute solutions, regardless of whether the increased concentration was produced by addition of chloride, sulfate, or nutrient salts to the basic solution. When root systems were divided between dilute and concentrated nutrient solution having osmotic pressures of 0.3 and 1.8 atmospheres, 1.86 times as much water was absorbed from the dilute as from the concentrated solution. To eliminate differences in size of root systems caused by differences in concentration of the solutions, the positions of the roots in the solutions were reversed every other day. When roots were divided between distilled water and concentrated nutrient solution, almost twice as much water was absorbed from the water as from the nutrient solution during the first 3 days; but this was soon reversed, because so much more root growth occurred in the nutrient solution than in distilled water. Long (1943) approach-grafted tomato plants, obtaining two root systems, which could be immersed in different solutions. Most of the water and the nutrients were absorbed through the root system in the less concentrated solution.

These results are to be expected if it is true that the intake of water is dependent on the gradient of free energy or diffusion-pressure deficit from substrate to root. Addition of solutes decreases the free energy and increases the diffusion-pressure deficit of water, thereby decreasing the steepness of this gradient. Eaton (1942) suggests that this is an oversimplification of the problem, because it is well

known that the concentration of solutes also increases in the tissues of plants grown on saline substrates. When six species of plants were grown in substrates having osmotic pressures ranging from 0.7 to 6.0 atmospheres, the difference between the osmotic pressure of the plant sap and that of the substrate averaged a little over 11 atmospheres. As great a diffusion-pressure-deficit gradient from substrate to root was maintained by the plants in the most concentrated solution as by those in the least concentrated solution. Plants transferred from dilute nutrient solution to more concentrated solutions often wilt at first but usually recover after a time. Hayward and Spurr (1943) found that roots which had been preconditioned by growth in a concentrated solution for several days absorbed more water from concentrated solutions than did roots transferred directly from the dilute-nutrient solution. Plants which grow in saline soils have plant saps with much higher osmotic pressures than those of plants growing in nonsaline soils. The highest osmotic pressures ever observed in plant saps were found in *Atriplex confertifolia,* a native of the Arizona salt flats (Harris, 1934). Even though an adequate gradient may be maintained from substrate to root, a much greater diffusion-pressure deficit exists in the tissues of plants growing in a concentrated solution, and this no doubt is responsible for their reduced growth. Long (1943) reported that on a warm, sunny day leaves of plants growing in a solution with an osmotic pressure of 0.7 atmospheres had a moisture deficit of 15 per cent, while those in a nutrient solution with osmotic pressure of 4.8 atmospheres had a deficit of 25 to 30 per cent. The accumulation of salt in the tissues also doubtless finally injures the tissue, but there are probably considerable differences between species with respect to the amount of salt tolerated.

Wadleigh, Gauch, and Magistad (1946) found that growth inhibition of guayule was closely related to the total moisture stress produced in the plants, whether this was produced by increasing soil-moisture tension obtained by dry-

ing a nonsaline soil, or was produced by increasing osmotic pressure of the soil solution through addition of salt.   Wad-
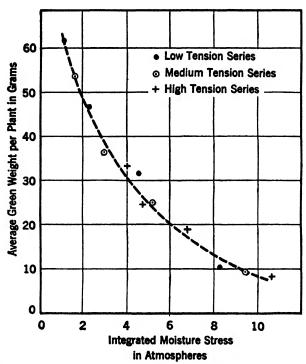
FIG. 35.   Effects of increasing moisture stress on growth of bean plants. Low-moisture-tension plants were watered when 40 to 50 per cent of the available soil moisture was removed.   Medium-tension plants were watered when 60 to 65 per cent of the available water was removed, and high tension plants were not watered until 90 to 100 per cent had been removed.   Each moisture series was subdivided into four groups, which received, respectively, no salt, 0.1 per cent, 0.2 per cent, and 0.3 per cent sodium chloride.   For example, the highest yield was in low-tension soil containing no salt and the lowest yield, in high-tension soil containing 0.3 per cent salt.   Reduction in yield was proportional to increase in average moisture stress, whether the increase was caused by low soil moisture or by high salt, or by a combination of the two.   (*From Wadleigh and Ayers, 1945*.)

leigh and Ayers (1945) found only small differences between bean plants grown under moisture stress produced by high soil-moisture tension or by high salt concentration of the soil solution (see Fig. 35).   They concluded that the

observed reduction in growth was caused largely by reduced hydration of the protoplasm resulting from inadequate absorption of water. It makes little difference whether reduced absorption results from high soil-moisture tension or from high osmotic pressure, so long as an internal water deficit results. Ayers, Wadleigh, and Magistad (1943) also state that reduced root elongation and reduced absorbing area of roots in saline soil are of considerable importance under field conditions. As was noted in Chap. 6, concentrated soil solutions reduce root elongation and cause rapid suberization, thus reducing the extension of roots into new soil areas and reducing their absorbing capacity.

Plant Factors Affecting Absorption

The principal plant factors which limit the intake of water are the extent and efficiency of the root system and the rate of transpiration. The rate at which water enters a particular root at a particular time is determined primarily by the permeability of the tissues of the root and by the steepness of the diffusion-pressure gradient from soil to root. Since the steepness of this gradient is determined largely by the rate of transpiration, the latter usually determines the rate of absorption, provided that water is available.

Efficiency of Roots

Nutman (1934) concluded that the intake of water by coffee trees is limited by the root surface. Water intake can be regarded as occurring in three steps: movement of water from soil to root, movement across the cortex, and entrance into the vessels. The vessels have a very small surface area compared with the root surface, and Nutman calculated that water must pass into the xylem 170 times as rapidly as it passes into the epidermis. He estimated the maximum rate of water movement into coffee roots to be 2.5 ml. per sq. m. per hour. Some additional data on the rate of movement of water into roots are presented in Table 7. All these measurements were made by enclosing roots in potometers, ex-

Table 7.   Rates of Entrance of Water into Roots

Investigator	Material and condition	Observed rate	Rate, cu. mm./ cm.^{2}/hr.
Hayward, Blair, and Skaling (1942)	Corn, young roots in water	0.2 mm.^{3}/mm.^{2}/hr.	20.0
Rosene (1941)...	Onion, young roots in water	Max. of 84×10^{-4} mm.^{3}/mm.^{2}/min.	50.4
Rosene (1943)...	Radish, root hairs	Max. of 31×10^{-4} mm.^{3}/mm.^{2}/min.	18.6
Hayward, Blair, and Skaling (1942)	Sour orange, suberized roots in water	0.3 mm.^{3}/mm.^{2}/6 hr.	5.0
Kramer (1946)...	Shortleaf-pine, suberized roots in water	3.37 mm.^{3}/cm.^{2}/hr.	3.37
Nutman (1934)..	Coffee tree, entire root system in soil	2.5 ml./m.^{2}/hr.	0.25

cept those for coffee, which were calculated from the rate of transpiration and the root surface of a tree. It is doubtful if these data can be regarded as anything more than very general indicators of differences in permeability, because they were obtained under very different conditions and with very different rates of transpiration. Nevertheless, the highest rates, as would be expected, are those for water movement into root hairs and epidermal cells of young unsuberized roots, and the lowest rates are for water movement into mature, suberized, woody roots.

The evidence seems contradictory as to whether or not root surface is commonly a limiting factor in absorption. Nutman believed it to be limiting in coffee trees. Plants growing in water culture or in moist soil often wilt on hot, sunny days; and this suggests that their root systems are unable to absorb water rapidly enough. On the other hand, considerable portions of the root systems of crop plants are sometimes destroyed by too-close or too-deep cultivation

without resulting in any serious wilting. Many grasses certainly have root surfaces in excess of what is necessary for adequate absorption. Weaver and Zink (1946a) reported that they were able to remove half or more of the root systems of certain grasses without injury to the plants. It seems likely that many trees have a less adequate absorbing surface than grasses have. Furthermore, a very large percentage of the surface of tree roots is suberized and less permeable to water than the young, unsuberized roots that are usually so abundant on herbaceous species. As was stated in Chap. 5, it appears that these roots are more permeable to water than is usually supposed, and it is probable that much of the water absorbed by trees enters through the older roots.

The Diffusion-pressure Gradient from Soil to Root

Since the diffusion-pressure deficit of soil near the field capacity is less than 1 atmosphere, and at the permanent-wilting percentage it is in the neighborhood of 15 atmospheres, in moist soil the magnitude of the diffusion-pressure gradient depends largely on the size of the diffusion-pressure deficit developed in the plant. At incipient wilting, the diffusion-pressure deficit is equal to the osmotic pressure of the cell sap and, if water loss is rapid enough to produce a state of tension in the hydrostatic system, the diffusion-pressure deficit may even exceed the osmotic pressure. The osmotic pressure probably ranges from 10 to 20 atmospheres in most plants of mesic habitats and is considerably greater in plants of habitats where a high moisture stress exists. Thus at incipient wilting, the diffusion-pressure deficit in the average plant probably amounts to 10 to 20 atmospheres, which is comparable to the diffusion-pressure deficit of approximately 15 atmospheres which usually exists in the soil at permanent wilting. There is some evidence that much larger diffusion-pressure deficits sometimes exist in transpiring plants. The reader may wonder why, if tensions of perhaps 100 atmospheres sometimes exist in plants,

absorption of water is reduced by a moisture stress of only 4 or 5 atmospheres and wilting occurs at an external diffusion-pressure deficit of only 15 atmospheres. The fact is that, even if a diffusion-pressure deficit of 100 atmospheres is developed in a plant, it will but slightly defer the onset of permanent wilting, because the diffusion-pressure deficit of soil in the vicinity of permanent wilting increases so much more rapidly than the diffusion-pressure deficit of the plant that water intake is soon stopped. This is easily seen by examining the curves in Fig. 3.

Protoplasmic Differences

Another plant factor which has never been thoroughly evaluated is the existence of hereditary differences in the permeability of protoplasm to water. The chief evidence for this is the fact that water intake is reduced to a different extent in different species by cooling the soil. Levitt and Scarth (1936) reported differences between species with respect to the effects of cold-hardening on permeability of the protoplasm to water and solutes. It was also observed that cold-hardened plants show less increase in viscosity of protoplasm when cooled than do nonhardened plants. Differences between species with respect to tolerance of poor aeration must, in at least some instances, depend on differences in reaction of protoplasm to low oxygen and high carbon dioxide. The existence of other basic physiological differences between roots and shoots of the same species has already been mentioned.

CHAPTER 10

THE ABSORPTION OF SOLUTES

It is scarcely possible to discuss the absorption of water without discussing the absorption of solutes. Most physiologists of the nineteenth century assumed that the intake of mineral nutrients from the soil was concomitant with and controlled by the intake of water. Since the minerals were known to occur in the soil solution, it seemed logical to suppose that they were carried into the roots along with the water. Presumably the only limitation on their entrance with the water was the degree of permeability of the root membranes. During the nineteenth century, permeability generally was regarded as a rather static phenomenon, comparable in most respects to the permeability of a nonliving membrane in an osmometer. Only in the latter part of the century was it realized that the permeability of living membranes varies under the influence of various factors that affect protoplasmic activity. Much research on permeability of plant membranes to solutes was carried on during the early part of the twentieth century, but not until recently has at least a partial understanding of the relation between permeability and solute absorption been attained. Before this problem is considered in detail, it seems desirable to discuss the relation between water and solute absorption.

Relations between Water and Solute Absorption

Near the beginning of the nineteenth century, De Saussure observed that plants absorbed proportionately more water than salts and absorbed more of some kinds of salts than of others. His views seem to have been neglected by later workers who, following the trend toward simple, physical

explanations, found it easier to believe that a close relationship existed between water and salt absorption. Schloesing's experiments were often cited as evidence of this. He grew three tobacco plants in the open and one plant under a bell jar. The salt content of the latter was much lower than that of the plants grown in the open, but Loomis (1929) pointed out that this plant was grown under conditions so different from those existing in the open that the plants should not have been compared and no valid conclusions were possible.

During the first quarter of the present century, a number of experiments were performed on a much larger scale. Miller (1938) has reviewed the research of Hasselbring, Kiesselback, Mendiola, Muenscher, and others; hence, only a brief summary will be given. In most of these experiments plants were grown with and without shade, or in high and low humidity, the results being very different rates of transpiration and of water absorption. A comparison of the quantities of water and of salt absorbed indicated that the quantity of salt absorbed was not proportional to the quantity of water absorbed. The results of these experiments have been criticized because plants grown in sun and in shade, or in high and in low humidity, are anatomically and physiologically different and cannot properly be compared.

In the more recent experiments of Freeland (1937) and of Wright (1939), this difference was obviated by growing all plants under the same conditions, so that they would be similar when the experiment was started. They were then divided into two groups, placed in containers of nutrient solution of known concentration, and exposed to high and low humidities for 3 or 4 days, a period believed to be too short to produce any serious anatomical or physiological changes which might affect their capacity to absorb salts. At the end of the experimental period, the volume of water absorbed was measured and the remaining solution was analyzed, to determine how much salt had been absorbed. In Wright's experiments, the bean plants, which had ab-

sorbed the most water, also had absorbed the most calcium, nitrogen, phosphorus, and potassium. Freeland studied bean and corn plants in a similar manner, and he too found that the plants which absorbed the most water absorbed the most salts as well. The increase in amount of salt absorbed was by no means proportional to the increase in amount of water absorbed by the more rapidly transpiring plants, however, and the rates of absorption of the various ions differed in the two species.

Hoagland (1944) and his associates, who have given this problem considerable attention, have concluded that transpiration and water absorption do not directly control the rate of salt intake. They found that solutes can be absorbed from a culture solution either more or less rapidly than water is absorbed, depending on the kind of solutes, the salt content of the plant, its sugar content, and the metabolic activity of the roots. In a series of experiments with young barley plants, nutrients were supplied in three different ways. One group was supplied continuously, another group was supplied only during the day, and a third group was supplied only during the night. All three groups of plants grew well, and the intake of nutrients was nearly the same in the plants supplied only at night, when water absorption was lowest, as in plants supplied only during the day, when water absorption was highest. In the summer, total salt absorption of plants supplied during the entire 24 hours was nearly twice that of plants supplied for only 12 hours; but in the winter, salt absorption in 24 hours was much less than twice that occurring in 12 hours. This was interpreted as indicating that salt absorption in the winter is limited by the smaller supply of carbohydrates resulting from the reduced photosynthesis at that season. In another, simpler experiment, a squash plant with roots in an unaerated bromide solution absorbed water, but very little bromide, and none was translocated out of the roots. A similar squash plant with well-aerated roots absorbed so

much bromide that it was translocated throughout the shoot.

The results of these and other experiments indicate that the amount of salt absorbed by a plant is determined by factors affecting its metabolic activity, rather than by the volume of water absorbed. As has been suggested by Broyer and Hoagland (1943), if the roots are injured in any way, the absorption of solutes will be more nearly proportional to the absorption of water. These investigators also suggest that, while variations in rate of transpiration appear to have little direct effect on salt intake, rapid rise of water in the xylem may expedite the translocation of minerals from the roots to the shoot. This might in turn increase the rate of absorption. After the minerals have entered the xylem, their upward movement depends largely on the speed of the transpiration stream. In one experiment on a bright sunny day, radioactive phosphorus that was supplied to the culture solution in which some large tomato plants were growing was detected in the tops of plants 6 ft. tall in 40 minutes (Arnon, Stout, and Sipos, 1940).

In general, it seems that, although the rate of transpiration can sometimes modify the rates of absorption and translocation of solutes in plants, it by no means controls these processes.

Absorption of Nutrients by Plants

The absorption of nutrients from the soil by plants is a very complex process, affected by numerous factors in the plant and in the soil. It has, therefore, been found more feasible to investigate the nature of the process by studying absorption in simpler systems, with the hope of applying the results to rooted plants. Much has been learned from studies with the algae Nitella and Valonia, from work with slices of such tissue as apple and potato, and especially from experiments with roots of barley. Because this work is too extensive to be reviewed in detail, only a summary of the important conclusions will be presented. For more de-

tailed accounts of current experimental work, the reader is referred to Hoagland (1944), to Steward (1935), and to numerous recent papers.

Permeability of Cells to Solutes

In the earlier work, chief emphasis was placed on the permeability of cells and tissues to various substances; but it soon became evident that the permeability of a cellulose cell wall is quite different in nature from the permeability of the protoplasmic membranes of a cell. The cell walls of plants, as well as many other membranes composed largely of nonliving tissue, are passively permeable in the sense that movement of materials through them is controlled largely by concentration gradients. Furthermore, their permeability is relatively stable and not much affected by small changes in composition of the solution. Some living animal membranes, such as the capillary endothelium, also show passive permeability, allowing ions to diffuse through along concentration gradients but preventing the passage of colloids (Krogh, 1946b). Most living membranes, however, show a high degree of differential permeability, and their permeability to various substances changes under the influence of various internal and external factors. Measured in terms of rate of penetration, permeability of living cellular membranes is low for such polar compounds as water, electrolytes, and carbohydrates, yet these substances move freely from cell to cell and from tissue to tissue in plants. Several ingenious theories of permeability have been developed to explain these facts, but they are not very useful in explaining the absorption of nutrients by plants.

Present evidence indicates that permeability in itself is not the most important factor affecting the absorption of solutes by roots. The extent to which a substance is accumulated in a cell or a tissue is now regarded as much more important than the rate of penetration of that substance through cell membranes. This became apparent when a distinction began to be made between rapidly growing tis-

SALT ACCUMULATION RELATIVE TO GROWTH AND METABOLISM
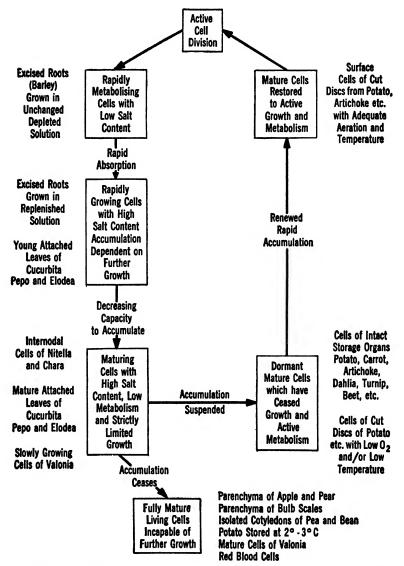
Fɪɢ. 36. Classification of representative types of plant tissues and cells with regard to their ability to accumulate inorganic solutes. (*From Steward, 1935.*)

sue, which has a large capacity to accumulate solutes, and mature tissue, which has little or no capacity to accumulate. Such differences in capacity to accumulate are shown in Fig. 36, taken from Steward (1935).

Diffusion of Solutes into Cells

It was long supposed that the intake of solutes by cells could be explained as a simple, physical process in which materials diffused from a region of higher concentration outside the cell or the tissue to a region of lower concentration within. Thus the nutrients in the soil were supposed to diffuse into the roots along a concentration gradient. This simple explanation of solute absorption proved totally inadequate, however, because improved techniques revealed that the concentration of various substances is often higher within the absorbing cells than it is outside. For example, Hoagland and Davis (1923) found 2,000 times as much potassium, 13 times as much calcium, and 870 times as much phosphate in the vacuoles of Nitella cells as in the pond water in which the Nitella was growing (see Fig. 37). It was suggested that accumulation could occur under such conditions, because the ions are absorbed, precipitated, or combined in some insoluble form in the cells, thus keeping the concentration in the cell sap very low. Study of the vacuolar sap of Nitella and other plants showed that the solutes occur in the vacuole largely in ionized form; hence, absorption actually occurs against a concentration gradient.

Similar processes take place in animal cells. Thus in the kidneys, salts are differentially absorbed and a dilute solution, the urine, is produced. Aquatic animals in general must absorb salts against a concentration gradient in order to live. Many examples of differential absorption and accumulation of solutes against a concentration gradient are known (Krogh, 1946b).

The evidence collected in recent years indicates that the mineral nutrients absorbed by plants do not diffuse in along concentration gradients and that they are not carried in

along with the water. It is evident that the absorption of solutes is brought about by a more complex process, the nature of which will now be discussed.
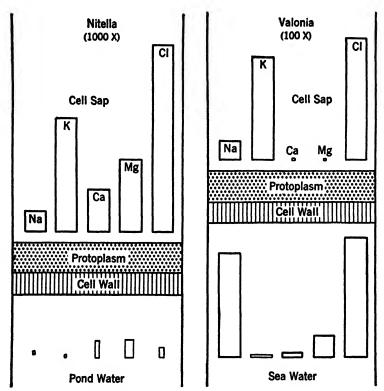
Fig. 37. Diagram showing relative concentrations of several ions in the surrounding medium and in the vacuolar sap of Nitella, a fresh-water organism, and Valonia, which lives in salt water. All of the ions reached a much higher concentration in the sap of Nitella than in the external solution. In Valonia, potassium was accumulated in excess of its external concentration, but not sodium, calcium, or magnesium. (*From Hoagland, "Inorganic Nutrition of Plants," 1944. Courtesy of Chronica Botanica Co.*)

Nature of the Absorption Process

It is generally agreed that the absorption of nutrient salts by plants depends primarily on the ability of the cells of the roots to accumulate them, and this requires the expenditure of energy. Much attention has been given to the na-

ture of this accumulation process, and considerable is known about the factors affecting it, although its exact mechanism is still unknown. Practically all workers agree that energy is expended by the cells in bringing about a transfer of solutes across the cytoplasmic membranes against a concentration gradient, but they do not agree on the manner in which it is expended.

Lundegardh and Burstrom (1933), who claim that anions are absorbed by the expenditure of energy, but not cations, postulated a basic rate of respiration, plus a special type, termed "Anionenatmung," which varies for different ions. Other workers, including Hoagland and Steward, believe that no unique type of respiration need be postulated and that there is no fundamental difference in the absorption of anions and cations. Brooks (1937, 1940) believes that solute intake is a two-stage process. The first step, which is physical, consists of adsorption of ions in or on the surface of the protoplasm by exchange with ions already present in the protoplasm; this is followed by their movement into the vacuole by a process requiring the expenditure of energy. The first part of this process appears to be almost instantaneous, but the second stage occurs much more slowly.

Jenny and Overstreet (1939) consider that ion exchange between soil colloids and roots is an important factor in the absorption of nutrients from the soil by plants. Overstreet and Jacobson (1946) reported that nonmetabolic absorption of radioactive rubidium and phosphate ions by barley roots occurred within less than a minute, even at near-freezing temperatures, which almost completely stop accumulation that depends on metabolic activity. The rapidity of absorption and the fact that it was not hindered by low temperature caused them to characterize it as nonmetabolic absorption, probably an exchange process of the sort already proposed by Brooks and others. Even if some sort of ion exchange constitutes the first step in absorption, the ions must be removed from the surface to the vacuoles of the

cells if there is to be any material increase in the total salt content of the roots.

It has been demonstrated by the use of radioactive potassium that some ions are moving out of cells while the cells show a net accumulation of that ion. Barley roots first placed in a solution containing radioactive potassium, then placed in distilled water, lost almost no potassium; but if they were placed in a solution containing nonradioactive potassium, considerable loss occurred, both at 20 and at 1.0°C. (Broyer and Overstreet, 1940). Outward movement occurred in the absence of oxygen, as well as at low temperature—an indication that it is quite different in nature from inward movement, which is inhibited by low temperature and by low oxygen. Perhaps the outward movement merely represents an exchange of ions with the surrounding solution, involving no expenditure of energy.

In view of the known facts, the following seems to be a reasonable outline of the absorption process. The first step is some sort of exchange process between ions on the surfaces of the root cells and those in the surrounding solution or on the soil colloids. Probably for the most part H^+ ions are exchanged for cations and OH^- or HCO_3^- ions for anions, though other ions might enter into this exchange. Jenny and Overstreet (1939) and others place much emphasis on direct contact between roots and soil particles in bringing about this exchange, but exchange with ions in the soil solution certainly occurs also. The adsorbed ions are then moved from the cell surfaces into the cell vacuoles by a process about which we know little, except that it requires energy and is closely related to aerobic respiration. We might call this process secretion, but that would not really add to our understanding of it, because we do not understand the nature of secretion. The ions must then be transported across several layers of cortical cells into the stele, and finally into the xylem vessels. Crafts and Broyer (1938) suggested that the outer cells of the cortex, being those that are best aerated, have the greatest capacity to

accumulate solutes. As the cortical cells are progressively less well aerated toward the stele, there is, from epidermis to stele, a gradient of decreasing ability to accumulate and hold solutes. Thus a concentration gradient is set up, along which solutes might move by diffusion, aided by protoplasmic streaming. The concentration of solutes in the xylem vessels is kept low by constant removal in the transpiration stream. Movement along such a gradient might be relatively rapid. Bromide ion was found in the xylem exudate of squash plants within 30 minutes after it was placed in the culture solution surrounding the roots. Crafts and Broyer suggests that more than half of this time may have been used in moving the ions across the protoplasm of the living cells which they traversed. Although this explanation of the absorption process is incomplete, it seems to be in accord with those facts which are now known.

Factors Affecting the Absorption of Solutes

Although there is not yet complete agreement as to the details of the mechanism of absorption, there is rather good agreement concerning the principal internal and external factors that affect the rate of absorption. The principal internal factors are the species of plant, the condition of the tissue, the absorbing zone of the roots, the internal concentration of salts, the concentration of sugar, and the rate of respiration. External factors include aeration, temperature, concentration and composition of the external solution, and pH. The effects of each of these factors will be discussed individually.

Species of Plant. Plants of different species differ widely in the amounts of various elements which they can absorb from a given soil or culture solution. Much information on this subject has been summarized by Miller (1938), but a few illustrations will be given. The ash of Andropogon grown on a sand dune contained 65.4 per cent of silica, while the ash of *Prunus pumila* from the same dune contained only 1.5 per cent of silica. Another extreme example is the

observation that, when grown on soil containing only 2.1 p.p.m. of selenium, *Astragalus bisulcatus* accumulated 1,250 p.p.m., while *A. missouriensis* accumulated but 3.1 p.p.m. from the same soil.

Collander (1941) made a careful study of cation absorption by 21 species of plants representing several families and ecological habitats. He found differences between species to be considerable for sodium and manganese, the maximum quantity absorbed being 20 to 60 times the minimum quantity. Differences were small for potassium, rubidium, and caesium, the maximum quantity absorbed being only two to three times the minimum quantity. The differences between species were constant and well defined, and obviously were genetic in origin.

Some of Collander's results are shown in Fig. 38. He could offer no explanation for the differences found. Some differences might be related to a difference in extent and type of root systems; but these factors would not have entered into his experiments, because he grew his plants in culture solutions. Apparently there are unknown differences in the absorption mechanism of various species.

Condition of Tissue. Actively growing tissues and organs, such as root and stem tips and young leaves, and various sorts of growing cells have been demonstrated to have a great capacity to accumulate solutes. On the other hand, mature tissues which are no longer growing, such as those of apple, carrot, pear, and other storage organs, and mature leaves have little or no capacity to accumulate solutes. They may exchange ions with a surrounding solution, but they seldom show any net accumulation. Some mature tissues, such as those of potato tuber, regain their ability to absorb solutes when sliced and placed in a well-aerated medium. The differences in behavior of various tissues are illustrated in Fig. 36. The significance of such differences in absorbing capacity, with reference to absorption of salts by roots, will next be considered.

Absorbing Zone of Roots. There is a tendency to consider any unsuberized root surface to be an absorbing sur-
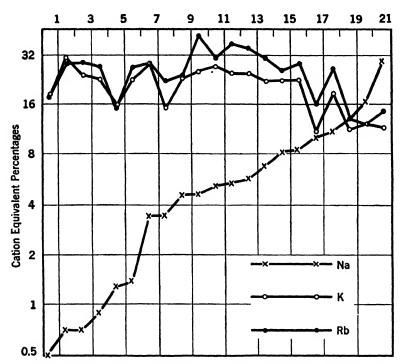
FIG. 38. Differences in amounts of various ions absorbed by different species of plants. The species are arranged according to increasing sodium content. Although there were wide differences in amount of sodium absorbed there was not much difference in the amounts of potassium and rubidium absorbed. (*From Collander, 1941.*)

The plants are arranged according to increasing sodium content.

1. Fagopyrum	8. Solanum	15. Melilotus
2. Zea	9. Spinacia	16. Vicia
3. Helianthus	10. Avena	17. *Atriplex litorale*
4. Chenopodium	11. Aster	18. Sinapis
5. Salsola	12. Papaver	19. Salicornia
6. Pisum	13. Lactuca	20. *Plantago maritima*
7. Nicotiana	14. *Plantago lanceolata*	21. *Atriplex hortense*

face for solutes, as it probably is for water. The surface through which absorption of solutes occurs appears to be much more restricted in area, however, than the surface through which water intake occurs, because it is determined

not by mere permeability of the epidermal cell walls but by the capacity of the cells to accumulate solutes. This conclusion is based on studies of the absorbing zone of barley roots made by Prevot and Steward (1936) and by Steward, Prevot, and Harrison (1942). They found that, in terms of unsuberized epidermal cells, the potential absorbing surface extends from the root apex to the point where secondary roots appear, but that the functional absorbing surface for solutes actually is restricted to a region near the apex. There is a longitudinal gradient, with most rapid intake in the apical 2 or 3 cm.

Overstreet and Jacobson (1946) reported that maximum absorption of rubidium and phosphorus occurred within the apical centimeter of the root, and that root hairs were not very active in the type of absorption with which they were dealing. These experiments possibly give an incomplete picture, because their short duration affords little opportunity to observe the effect of removal of solutes from the root by the growing shoot. Steward, Prevot, and Harrison found that, when plants were placed in tap water, ions were first removed by the shoot from those portions of the root which had originally been most active in absorbing them, and they were removed from the cortical cells of the older part of the root much more slowly—perhaps, at least in part, because the endodermis prevented their direct transfer into the xylem. Possibly they eventually moved in through the branch roots which pierced the endodermis.

The location of the gradient in solute absorption agrees with the location of the gradients in respiratory activity of roots observed by Gregory and Woodford (1939) and by Machlis (1944). Their studies indicate that respiration is most active at the root tip and that it decreases toward the base.

It would be interesting to determine the zone of maximum water intake in these roots, as well as the zone of solute intake. Studies on water absorption mentioned in Chap. 5 indicated that in onion and corn roots maximum water

absorption occurs several centimeters back of the root apex (see Fig. 15).

Although the intake of minerals through growing root tips doubtless provides a sufficient supply for most herbaceous plants, with their continuously growing root systems and numerous root tips, it seems inadequate for many woody plants. As was noted in Chap. 5, trees pass through long periods during which little root growth occurs, and they almost certainly absorb considerable quantities of water through the suberized regions of their roots. It seems probable that some intake of minerals must occur also. Perhaps these are passively transported in the water, without any accumulation in living cells or any expenditure of energy, as occurs in root tips. One of the few pieces of evidence bearing on this is the report of Chapman and Parker (1942) that orange roots which were at least partly suberized absorbed considerable nitrate.

Roots which have been injured or killed lose their differential permeability and their ability to accumulate solutes; but as long as water intake occurs through them, salts almost certainly are carried into the xylem in the water. Broyer and Hoagland (1943), studying salt absorption by roots that had been injured by an excessive concentration of sodium chloride, concluded that such roots absorb passively, intake being controlled by water movement rather than by their metabolic activity. Another example is the passive absorption of bromide through tomato roots that had been injured by a high concentration of carbon dioxide, as reported by Hoagland and Broyer (1942).

Internal Concentration of Salts. Although the absorption of solutes commonly occurs against a concentration gradient, it is not independent of the steepness of the gradient. Excised roots initially low in salt content absorb ions much more rapidly at first than do roots that have an initially high salt content, but the rate of absorption decreases as the ions accumulate. Accumulation continues at a higher rate in attached roots than in detached roots, be-

cause the ions are removed from the root by the shoot as they are absorbed. The shoot also supplies the root with sugar and possibly with hormones, which have a stimulatory effect upon absorption.

Concentration of Sugar. Reference to the relation of the shoot to absorption by the roots leads to mention of the importance of an adequate supply of sugar in the roots. Cells and tissues low in sugar do not accumulate solutes as rapidly as those which are high in sugar. It has been pointed out by Steward and others that failure to take into account the past history of tissue used in absorption studies, especially with respect to the sugar and salt content, can result in erroneous conclusions. A tissue might be regarded as rather impermeable to a certain solute, although failure to show accumulation was really the result of low metabolic activity caused by low sugar content. Eaton and Joham (1944) suggested that much of the decline in mineral intake which accompanies heavy fruiting of cotton can be attributed to the reduced movement of carbohydrates to the roots.

Rate of Respiration. Throughout this discussion, the fact has been emphasized that there is a close relationship between metabolic activity and ability to absorb and accumulate solutes. Another thing that has been made clear is that the gradient of respiratory activity in roots closely parallels the gradient of capacity to accumulate ions. At one time it was supposed that the carbon dioxide released during respiration played an important part in salt absorption; but this is not necessarily true, because no salt accumulation occurs in the absence of oxygen, though considerable carbon dioxide may be released. It is the energy released by respiration that is essential for the movement of solutes across the cytoplasmic membranes into the vacuoles of cells. While accumulation of solutes is dependent on the occurrence of aerobic respiration, the two processes are not necessarily proportional. Many storage tissues in which respiration is occurring rapidly will accumulate little or no solute because they are no longer growing. Nevertheless, if res-

piration of actively accumulating tissue is decreased by chemical inhibitors, low temperature, or inadequate oxygen supply, the accumulation of solutes is invariably decreased or stopped.

The absorption of solutes, the active absorption of water leading to the development of root pressure, the synthesis of organic acids and of proteins, and the rate of aerobic respiration are, it seems, rather closely related phenomena.

Aeration. The retarding effects of inadequate aeration on root growth were discussed in Chap. 6; its effects on absorption of water, in Chap. 9. By this time it should be understood that lack of adequate aeration of roots interferes even more seriously with the intake of minerals than with the intake of water. Hoagland and Broyer (1942) studied the effect of aeration of the roots on intake of bromide ions through tomato-root systems attached to a vacuum line. In well-aerated solutions, the concentration of bromide was higher in the exudate than in the solution surrounding the roots. In solutions saturated with carbon dioxide and with nitrogen, the intake of bromide ion was reduced, but the effects of carbon dioxide were observed sooner. Furthermore, the concentration of bromide ions in the exudate from root systems exposed to carbon dioxide rose until it became equal to that of the external solution, but this did not occur in the case of root systems exposed to nitrogen. The reason would seem to be that carbon dioxide produces more rapid changes in metabolic activity, permeability, and ability of cells to accumulate ions than does deficiency of oxygen. The results of this experiment are shown in Fig. 39.

Arnon and Hoagland (1940) concluded that inadequate soil aeration is often a limiting factor in the growth of crop plants, because lack of sufficient aeration retards the absorption of essential nutrients from the soil. As was indicated in Chap. 9, some species are affected more than others are. Rice, for example, thrives in saturated soil, while tomato requires the best possible aeration to ensure maximum absorption and maximum growth. Aeration requirements are

somewhat related to temperature, better aeration being required at high soil and solution-culture temperatures than at low temperatures. According to Lawton (1946), poor
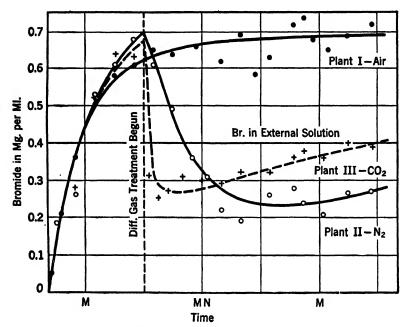
FIG. 39. Effects of nitrogen and carbon dioxide on composition of exudate from stumps of tomato plants to which suction was applied. Exposure of roots to nitrogen and carbon dioxide at first reduced the concentration of bromide ion in the exudate, but intake by roots exposed to carbon dioxide later increased until concentration in exudate was equal to that in the external solution. Apparently lack of oxygen first decreased permeability and ability of root cells to accumulate bromide, but later the roots exposed to carbon dioxide were so severely injured that bromide ion was carried in along with the water. (*From Hoagland and Broyer, 1942.*)

aeration retards potassium absorption by corn more than it does the absorption of other elements.

Temperature. Many demonstrations have indicated that the absorption of solutes is reduced by low temperature. Presumably this is, to a great extent, because reduced respiration releases less energy for that part of the absorption process which requires the expenditure of energy; but

doubtless other factors, such as increased viscosity of the protoplasm and reduced mobility of ions, are also operative. It is difficult to separate the effects of low temperature on the absorption process from its effects on translocation and on utilization of the nutrients in the plant. Little is known concerning the extent to which reduction of nutrient absorption by low soil temperature hinders plant growth. It may be a limiting factor on the growth of some crops in the spring and on alpine and arctic plants; but low temperature retards growth in a number of ways, and it is difficult to distinguish them from one another.

Concentration and Composition of the External Solution. The intake of a solute by tissues that have a high accumulative capacity, such as growing roots, is affected by the concentration of that solute in the solution from which absorption is occurring. For example, the rate of absorption of potassium by barley roots low in salt increased with the concentration of potassium in the external solution up to about 5 milliequivalents per liter, but absorption was not increased by further increase in concentration.

One of the problems to be solved in agriculture is to determine what concentration of nutrients should be maintained in the soil in order to ensure good growth of crop plants. Determination of the amounts of various elements present by chemical analysis is not very helpful, because it gives no indication of the amount which is available to plants. Most of the phosphorus and· some potassium are combined and held in an unavailable form, and chemical and biological reactions continually alter the concentration and availability of the various elements. In spite of these difficulties, some progress has been made in the use of chemical tests which indicate the concentration of various elements in soil extracts obtained by a certain method. Extensive experience has made it possible to state what range of concentration of the various nutrients, as indicated by these tests, is required for good growth of certain crops. Soil tests of this

type are now being used extensively in the growing of greenhouse and truck crops.

Much of our knowledge concerning the nutrient requirement of plants has been obtained from sand and solution cultures in which the composition and the concentration can be rigorously controlled. The results of these experiments
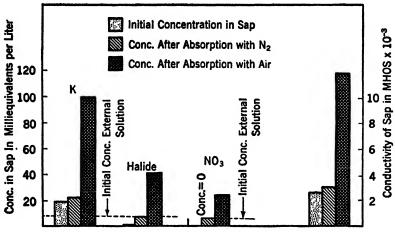
Fig. 40. In the absence of oxygen, barley roots are unable to accumulate potassium, halide, or nitrate ions; but when properly aerated, they accumulate all three in excess of the concentration in the external solution. (*From Hoagland, "Inorganic Nutrition of Plants," 1944. Courtesy of Chronica Botanica Co.*)

indicate that there is no one best solution for the growth of a given species of plants, but that plants can be grown successfully in solutions containing various concentrations of the essential elements, as long as the concentration of no element falls so low as to be limiting. The total concentration of salts that can be supplied to plants is limited by the fact that the osmotic pressure of a soil or of a culture solution should not exceed 2.0 to 2.5 atmospheres (see Chap. 3).

The amount of a particular element absorbed often is affected by the concentration of other elements present. If an abundance of potassium is available, for instance, less calcium and magnesium will be absorbed per unit of plant

tissue than if potassium is low; and to a lesser extent, high calcium and magnesium decrease potassium absorption from a medium low in it. Collander (1941) gives other examples of such effects. As the complexities of interactions of this kind are somewhat beyond the scope of this work, the reader who wishes more details is referred to Hoagland (1944), Miller (1938), and others.

pH. One of the most frequently measured properties of soils and culture solutions is their pH, and its influence on the availability of nutrients has often been stressed. In very acid soils aluminum, iron, and manganese sometimes become so soluble that injury to plants results, while calcium, nitrogen, and phosphorus become less available. The poor growth of many species of plants on very acid soil is often attributed principally to the toxic effects of an excessive concentration of aluminum in the soil solution. In very alkaline soils iron, manganese, and phosphorus become so insoluble that plant growth is often limited by deficiencies of one or more of these elements. The best soil pH for most crops is in the range between pH 5.5 and 7.0 because nutrients are most available in this range.

It should be emphasized that, over a wide range, the pH of the medium has little effect on the absorption process but acts through its effects on the availability (chiefly the solubility) of the various elements. Arnon and Johnson (1942) found it possible to grow plants over a pH range from 4 to 9, if special precautions were taken to ensure that all the essential elements remained in solution. Plants failed to grow at pH 3 because, according to Arnon, Fratzke, and Johnson (1942), no calcium or phosphorus was absorbed and the intake of other ions was much reduced. Phosphate absorption also was reduced at pH 9.

CHAPTER 11

ABSORPTION DEFICITS AND THEIR EFFECTS ON PLANTS

That absorption of water is only one of several closely interrelated processes comprising the field of plant-water relations is a point that must be emphasized. It is important, therefore, that this process should not be considered alone, but in relation to the other conditions and processes affecting the internal water relations of a growing plant. The most important phase of plant-water relations with respect to plant growth is the degree of turgidity maintained in the tissues, because loss of turgidity interferes with plant growth in a number of ways. Rapid transpiration is not harmful in itself, if it is accompanied by absorption sufficiently rapid to prevent serious internal water deficit or loss of turgidity from resulting. On the other hand, relatively slow transpiration can produce injurious water deficits if the rate of absorption is very slow, as when the soil is cold or dry. The ratio of absorption to transpiration, therefore, is more important than the absolute rate of either process. It has been stated previously that the rate of absorption of water generally is determined largely by the rate of water loss. Nevertheless, the two processes often proceed at different rates, at least for short periods of time, producing considerable fluctuations in the water content and the turgidity of plant tissues.

Terminology

Because of some obvious similarities to financial transactions, there has been a tendency to discuss plant-water rela-

tions in terms similar to those used in bookkeeping. This is both convenient and logical, as we may regard the water content of a plant as the water balance, which fluctuates according to the relation between transpiration expenditures and water-absorption income. If transpiration exceeds absorption, a water deficit results, which can be liquidated only if absorption subsequently exceeds transpiration. This terminology has been used extensively by European writers, Montfort (1922) and Maximov (1929), for example, who commonly employ such terms as "water balance," "water deficit," and "water economy" (*Wasserhaushalt*). It has been suggested that we are less concerned with the quantity of water used by or available to plants than with the condition of the water in the plant itself, the *Wasserzustand*. Walter (1931) coined the word *Hydratur* to refer to the condition of the water in cells and tissues as measured by its vapor pressure. The term "diffusion-pressure deficit" serves the same purpose, because it expresses the difference between the diffusion pressure of water in a cell or a tissue and the diffusion pressure of free water at the same temperature. Measurement of the diffusion-pressure deficits of plant tissues, therefore, affords quantitative information concerning the condition of the water in the tissues. For detailed discussions of the diffusion-pressure-deficit concept and its applications, the reader is referred to Crafts, Currier, and Stocking (1949) and to Meyer (1938, 1945).

Relative Rates of Absorption and Transpiration

There are several kinds of evidence indicating that on days favorable to transpiration the absorption of water lags behind water loss. Anyone who has observed growing plants has noted that on clear, warm days they frequently wilt near midday. While such temporary wilting is more noticeable and prolonged in dry soil, it often occurs in plants rooted in soil that has a moisture content near field capacity—occasionally, even in plants growing in well-aerated water cultures. Periodic measurements of leaf moisture show that,

even when no wilting takes place, the moisture content often is markedly reduced during the middle of the day. Direct, simultaneous measurements of absorption and transpiration also show that absorption frequently lags behind transpiration near midday.

The first simultaneous measurements of water intake and water loss known to the writer were made by Vesque (1878). By measuring absorption and transpiration of plants with their root systems in potometers, he found that transpiration exceeds absorption during the day and that absorption exceeds transpiration at night. Lloyd (1912) reported that transpiration from cut branches of *Fouquieria splendens* exceeded water intake during the day, but that at night absorption exceeded water loss. Stefanoff and Stoickoff (1932) compared absorption and transpiration of cut branches of a number of woody species and found that absorption lagged considerably behind transpiration in some species, but very little in others. Experiments on cut stems are unsatisfactory because of the probability that the water-conducting systems will become partially plugged with air or other substances and that thus free absorption will be prevented. Furthermore, cut branches are free from competition with other branches on the same plant and free from resistance to water movement into the roots; and they are better exposed to light and air. Hence, the rate of water intake of a separate branch may be quite different from the water intake of the same branch while it is attached to a plant.

Measuring the absorption of water from soil directly is impossible; but Livingston and Hawkins, using autoirrigators in the manner first suggested by Transeau (1911), measured the rate of absorption of plants, plus the soil surrounding their roots. The author (1937) used the autoirrigator method for measuring transpiration and absorption of several species of plants. Gallon metal cans were filled with soil and autoirrigator cones were buried in the center of the soil mass. Two plants were grown in each container,

located on opposite sides and as near the autoirrigator cone as possible. The irrigator cones were connected to bottles of water by flexible rubber tubing, and the bottles were
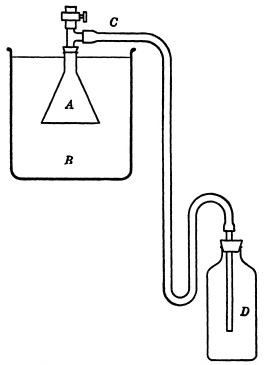
Fig. 41. An autoirrigator installation used to measure absorption by transpiring plants. The porous porcelain autoirrigator cone (A) is placed in the center of a gallon can (B) filled with soil, in which the plants are grown. A T tube is placed in a rubber stopper in the top of the irrigator cone and one arm is connected to the reservoir (D) by a piece of rubber tubing. The top of the T tube is closed by a screw clamp (C) on a piece of rubber tubing. This provides a means of removing air bubbles.

placed about 40 cm. below the plant containers, to prevent overwatering. With this arrangement, shown in Fig. 41, as the plant absorbs water from the soil surrounding the irrigator cone, water moves into the soil from the irrigator, which is kept filled from the reservoir by atmospheric pressure. The volume of water lost is determined by weighing

the plant container, plus the water reservoir; while the volume absorbed is determined by measuring the amount of water required to refill the reservoir up to a mark on its neck. If, for example, 20 ml. of water are required to refill the reservoir, and the entire system then weighs 10 gm. less than at the previous weighing, the plant, plus soil, has lost 30 gm., but has absorbed only 20 gm. If, on the other hand, 20 ml. of water are required to fill the reservoir and the system then weighs 10 gm. more than at the previous weighing, the plant—plus soil—has lost only 10 gm., but has absorbed 20 gm. Some error occurs because, when absorption is rapid, water probably is not supplied to the soil as rapidly as it is removed by the roots. This results in a decrease in moisture content of the soil, as well as in moisture content of the plant. If the soil mass is comparatively small and most of the roots are in close proximity to the irrigator, the error or lag resulting from change in moisture content of the soil probably is small. Data obtained by this method are presented in Fig. 42. Absorption lagged behind transpiration to about the same extent in all species, no difference existing between the woody, the herbaceous, and the succulent species studied.

In general, the rate of transpiration increases rapidly during the morning and attains a maximum by early afternoon, while the rate of absorption increases more slowly and reaches its maximum later in the afternoon. In the late afternoon, the rate of transpiration decreases more rapidly than the rate of absorption, and absorption usually exceeds transpiration during the entire night. Opuntia was a partial exception to the general rule, because the period of maximum transpiration occurred much later in the day; but the absorption curve was correspondingly displaced, so that it occupied the same position relative to the transpiration curve as it held in the other species. Sunflower plants and rooted willow cuttings grown in nutrient solution were found to behave much like plants growing in soil, transpiration ex-

ceeding absorption during the day and absorption exceeding transpiration during the night.

The shapes and relative positions of the curves for absorption and transpiration can be explained as follows.   In the
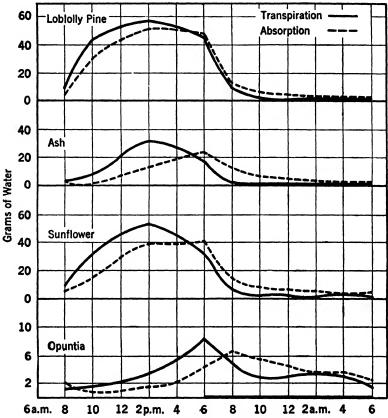
Fɪɢ. 42.   Average rates of transpiration and absorption of four species of plants on a bright, hot summer day.   (*From Kramer, 1937.*)

morning, when the stomates open and when leaf and air temperatures rise, the steepness of the vapor-pressure gradient from the intercellular spaces to the outside air increases, and transpiration increases rapidly.   Absorption does not increase, however, until the diffusion-pressure deficit developed in the cells of the leaves by water loss is transmitted

to the absorbing surfaces of the roots—a process that requires considerable time. In the late afternoon, as the temperature decreases and the stomates close, transpiration decreases rather rapidly, but absorption continues until the diffusion-pressure deficit existing in the plant tissues is completely satisfied; hence some absorption often occurs even in the early morning, when water loss is negligible.

Causes of the Absorption Lag

The existence of such a well-defined lag of absorption behind transpiration indicates that the diffusion-pressure deficit produced in the mesophyll cells of the leaves by transpiration is not instantly transmitted to the roots. Even after the deficit is transmitted to the roots, there evidently is considerable resistance to water absorption and movement, as is indicated by the development of appreciable water deficits in plant tissues and reduced pressure, or tension, in the water-conducting systems. Since the absorption lag is so well defined, even in plants growing in moist soil or in well-aerated water cultures, it cannot result from an inadequate supply of water in the environment, but must be caused by resistance to water movement within the plant. Wilson and Livingston (1937) compared the length of the lag period in willow cuttings with long and with short stems and concluded that in the plants with the longest stems not over 16 per cent of the lag could be attributed to stem resistance. They attributed the remainder of the lag to resitance to water movement through the parenchyma cells of the leaves and the roots. The writer believes that most of the lag is caused by resistance to water movement across the cortex of the root. It was found that duration of the lag period of tomato and sunflower plants having their root systems immersed in water was decreased by at least 50 per cent when the roots were removed.

Another kind of evidence that the roots offer considerable resistance to water movement is afforded by the behavior of wilted plants. Intact wilted plants usually require a half

hour or more for recovering when the soil around their roots is thoroughly wetted; but if the stems are bent over and cut under water, the leaves ordinarily recover their turgidity in less than 5 minutes. On anatomical grounds, the resistance to water movement through the leaves would be expected to be much less than the resistance in the roots. According to Mer (1940) and Wylie (1938), resistance to water movement through a living cell is much greater than resistance to water movement through even the smallest veins of the leaf. Most of the parenchyma cells in the leaves are separated from the xylem elements of the smaller veins by only a few cells, but in the roots of most plants water must cross a layer of 10 to 20 or more cortical parenchyma cells, the endodermis, and the pericycle, in passing from the epidermis to the xylem. Thus the diffusion-pressure deficit produced in the leaf mesophyll by transpiration is rapidly transmitted across the few intervening cells to the xylem of the small veins which supply the leaf blade with water, but considerable time is required to transmit the deficit across the cortex to the epidermis of the roots. Although the walls of the cortical cells offer some resistance, most of the resistance to water movement is produced by the protoplasm. This is indicated by the fact that much more water will pass through dead roots than would pass through the same roots while alive under similar conditions of time and pressure.

The amount of resistance of roots to water movement is further indicated by an experiment in which stems of sunflower plants were attached to a vacuum pump while the roots were immersed in water. After the rate of water movement had been measured for 30 minutes, the roots were cut off. The rate of water movement through the stems during the next 30 minutes was 80 times as great as before the roots were removed (Kramer, 1938). After studying a number of woody and herbaceous species, Warne (1942) also came to the conclusion that resistance to water movement through the stems is much less important than resistance to entrance of water into the roots. Probably

considerable resistance exists in those water-conducting systems which are interrupted by meristems, as the bases of leaves and internodes of monocots, and which are elongating rapidly.

Under some circumstances, the lag of absorption behind transpiration is caused in part by lack of sufficient root surface. The wilting of recently transplanted plants obviously is caused by reduction in absorbing surface. Transplanted trees and shrubs commonly are pruned, to bring the transpiring surface back into more nearly the same ratio to the absorbing surface as existed before transplanting occurred. Aldrich and Work (1934) found that, when the ratio of root surface to leaf surface, in pears, was increased by the removal of part of the leaves, the midday water deficit in the fruits and the remaining leaves was reduced. When the ratio of root surface to leaf surface was decreased by the removal of some roots, the internal water deficit was increased (see Fig. 43). The investigators concluded that, when the readily available soil moisture is reduced to 35 or 40 per cent of the total, the moisture supply to the leaves during periods of high transpiration is limited by the root surface. Nutman (1934) concluded that water intake by coffee trees is limited by their root system. On the other hand, there are many instances where a considerable fraction of the root system can be removed without serious consequences (see Chap. 9).

Diurnal Fluctuations in Moisture Content

Because of the daily lag of absorption behind transpiration, a daily cycle of variation in water content of the tissues of transpiring plants occurs. When transpiration is rapid, the midday decrease in turgidity often is great enough to cause visible, though temporary, wilting; but even when no wilting occurs, measurable decreases in moisture content, especially in leaves, can be observed. Livingston and Brown (1912) found that the difference between maximum and minimum leaf moisture content of certain desert shrubs

averaged 30 per cent of the maximum water content. Maximov and Krasnoselsky-Maximov (1924) reported that even in the cool, humid climate of Leningrad a midday deficit of 28 per cent of the maximum water content occurred in Helianthus and a deficit of 22 to 26 per cent in potato. The
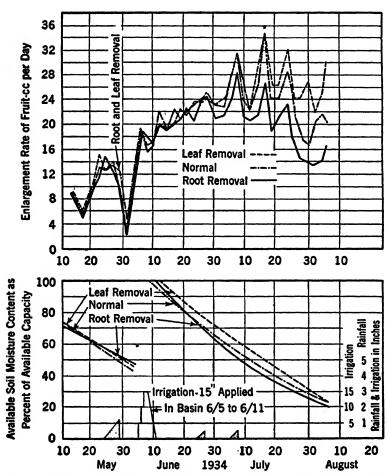
Fig. 43. Effects of changing the ratio of root surface to leaf surface on rate of enlargement of pears. As the soil moisture was reduced, the fruit on trees from which one-fifth of the roots had been removed showed greatest reduction in rate of enlargement. Fruit on trees from which one-fifth of the leaves had been removed showed least reduction. (*From Aldrich and Work, 1934.*)

only plant in which they observed no deficit was *Alisma plantago,* growing in a pond of water. The writer observed a minimum moisture content in leaves of autoirrigated Helianthus which was 35 per cent less than the maximum moisture content.

Decrease in the water content of leaves during the day,
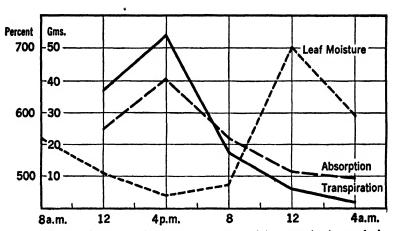
FIG. 44. Variations in leaf-moisture content and in transpiration and absorption rates of autoirrigated sunflowers. Leaf moisture is expressed as percentage of dry weight; absorption and transpiration, in grams of water per plant.

followed by an increase during the night, has been reported by a number of investigators, including Herrick (1933), Kramer (1937), Miller (1917), Runyon (1936), Stanescu (1936), and Wilson (1941). In general, the time of minimum leaf moisture content coincides with the time of maximum transpiration, but maximum leaf moisture content often occurs during the middle of the night, then decreases toward morning, instead of reaching a maximum about sunrise, as might be expected (Fig. 44). Although this anomalous behavior has been observed by several investigators, no adequate explanation has been offered. Possibly toward morning the leaves lose water to other organs of the plant, most likely to the stem. This might also be related to the

translocation of carbohydrates out of the leaves, causing the changes in diffusion-pressure deficit which result in redistribution of water.

It appears that the degree of wilting is not an accurate indication of the actual water loss or of the magnitude of the water deficit of leaves, because the amount of water which must be lost to cause wilting varies in different species. Many leaves, such as those of holly and pine, contain so much lignified tissue that even though the parenchyma cells lose their turgor the blades do not droop or roll noticeably. Even in leaves composed largely of thin-walled parenchyma, differences in reduction in moisture content necessary to cause wilting occur. Maximov and Krasnoselsky-Maximov found that some shade plants wilt when only 3 to 5 per cent of the total water content is lost, while sun plants can lose 20 to 30 per cent of their moisture content before wilting. Knight (1922) observed that leaves of the shade plant *Eupatorium adenophorum* wilted when the water content decreased only 1 per cent of their fresh weight. Krasnoselsky-Maximov (1925) found that in shade plants cell volume was reduced only 1 to 3 per cent during plasmolysis, but that in sun plants the reduction in cell volume amounted to 25 to 30 per cent. Thus a very slight loss in water content causes complete loss of turgidity and wilting in leaves of shade plants, whereas a considerably larger water loss from the leaves of sun plants is required to cause visible wilting.

Moisture content sometimes is expressed on a fresh-weight basis, but a dry-weight basis is more satisfactory because it fluctuates less. Even the dry weight varies somewhat, largely because of variations in carbohydrate content resulting from photosynthesis and translocation. Care should be taken to select leaves of similar age and exposure for measurement of diurnal changes in moisture content.

Development of a midday water deficit also results in a decrease in thickness and area of leaves. Thoday (1909) found that in bright sun the leaf area might be reduced 5 to 7 per cent, the greatest shrinkage occurring toward the

tip of the leaf and in older leaves, as compared with younger leaves. Bachmann (1922) devised a delicate instrument to measure changes in the thickness of leaves of less than 2 microns and, by its use, observed diurnal shrinkage even with low rates of transpiration.

Simultaneous sampling of roots, stems, and leaves of herbaceous species by Boggess and by Wilson (Wilson, 1941) showed large decreases in moisture content of stems and roots, as well as of leaves, during the day and increases at night. The range of variation was least in roots and less in stems than in leaves.

Variations in Osmotic Pressure and in Diffusion-pressure Deficit

Associated with the daily variation in moisture content of plant tissues are daily variations in osmotic pressure and in diffusion-pressure deficit of the tissues. Such variation in osmotic pressure, observed by many investigators, has been attributed partly to changes in carbohydrate content and partly to changes in moisture content. Stoddart (1935) observed a variation from an afternoon maximum of over 27 atmospheres to a nighttime minimum of less than 21 atmospheres in the leaf sap of *Andropogon scoparius* growing in dry soil. A smaller range of variation was observed in grasses growing in moist soil. These changes were almost perfectly correlated with changes in moisture content, which indicates that they were caused by variation in water content of the leaf rather than by variation in solute concentration. Seasonal changes in osmotic pressure also are common, being associated with changes in the age of tissues, the solute concentration, and the water content (Crafts, Currier, and Stocking, 1949; Miller, 1938).

More important than changes in moisture content or osmotic pressure are changes in diffusion-pressure deficit, because the latter controls the distribution of water in the tissues of the plant. As the moisture content of the leaves decreases, the concentration of the cell sap increases and the

cell volume and wall pressure decrease. The combined effect of these changes is to increase the diffusion-pressure deficit and thereby to increase the movement of water into the leaves. Later in the day, as transpiration slows down, the increasing moisture content and cell volume cause a decrease in osmotic pressure and an increase in wall pressure, which produces a decrease in diffusion-pressure deficit.

According to Crafts, Currier, and Stocking (1949), a considerable fraction of the total diffusion-pressure deficit may be caused by the high tensions produced when transpiration greatly exceeds absorption. As the diffusion-pressure deficit is affected by so many factors, it varies considerably more than does the osmotic pressure. Herrick (1933) measured the osmotic pressure and the diffusion-pressure deficits of leaves of *Ambrosia trifida* at various times of day. Both osmotic pressure and diffusion-pressure deficit of leaves at various heights on the plants increased during the day to a maximum in the afternoon, when the diffusion-pressure deficits were approximately equal to the osmotic pressure. Late in the afternoon, both values began to decrease. Some of his results are shown in Fig. 45.

Internal Movement of Water in Plants

If a well-watered plant were surrounded by a saturated atmosphere so that transpiration would be negligible, its cells presumably would become fully turgid and their diffusion-pressure deficit would become zero. Such a static condition rarely if ever exists. As a result of water loss by transpiration, changes in kind and concentration of solutes, turgor changes, and growth, it is likely that the amount and concentration of water and its diffusion-pressure deficit are continually undergoing changes in the various tissues and organs of a plant. Because these changes do not occur at the same rate in various parts of the plant, the diffusion-pressure deficit of one part of the plant often increases more rapidly than that of another part. As the movement of water from cell to cell always occurs along gradients of diffu-

sion-pressure deficit, this results in redistribution of water within the plant.

Considerable variations in osmotic pressure and in diffusion-pressure deficit occur among the various organs and tissues of plants. Leaves usually have higher osmotic pressures than roots do, and the higher leaves on a plant usually
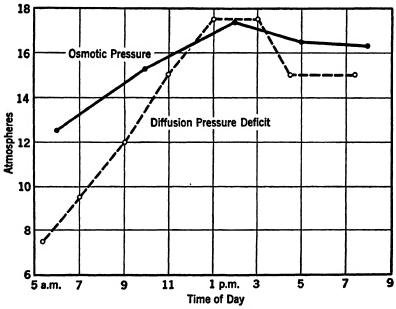
FIG. 45. Variations in osmotic-pressure and diffusion-pressure deficits of uppermost leaves of *Ambrosia trifida* on a hot summer day. (*From data of Herrick, 1933.*)

have higher osmotic pressures than the lower leaves have. Leaves exposed to the sun usually have higher osmotic pressures than shaded leaves have. According to Chandler (1914), the osmotic pressure of leaves usually exceeds that of green fruits on the same tree.

It is not so well known that even larger variations in diffusion-pressure deficit occur. These are possible because the diffusion-pressure deficit of a cell can vary from zero, when it is fully turgid, to a value exceeding the osmotic

pressure of its cell sap at incipient plasmolysis. When the tension on the water in the xylem elements exceeds the osmotic pressure of the sap of the living cells, the latter also is thrown under tension, and this results in the cells' developing diffusion-pressure deficits in excess of their osmotic pressures. Chu (1936) claims that the diffusion-pressure deficits of the leaves of trees depends more on tension in the water-conducting system than on the osmotic pressure of the cell sap. MacDougal, Overton, and Smith (1929) estimated that tensions up to 200 atmospheres exist in the water-conducting systems of transpiring trees; and Arcichovskij and Ossipov (1931) measured a diffusion-pressure deficit of 142.9 atmospheres in a desert shrub. As the water forms a continuous hydrostatic system through the water-saturated cell walls, the living cells of the root are presumably under equally high tensions and, therefore, develop very large diffusion-pressure deficits.

As has already been stated, movement of water occurs along gradients of diffusion-pressure deficit rather than along gradients of osmotic pressure. Thus water will move from any region where the diffusion-pressure deficit is low to one where it is higher, regardless of the relative osmotic pressures of the cells in the two regions. As long as the plant is well supplied with water, differences in diffusion-pressure deficits are small and all tissues obtain adequate water. When transpiration exceeds absorption, particularly if this occurs for several successive days, a serious water deficit develops in the plant, accompanied by severe competition for water between the various organs. As a result, those tissues which can develop the highest diffusion-pressure deficits, such as the more exposed leaves, obtain water at the expense of those that have lower diffusion-pressure deficits. On plants suffering from drought, the older leaves almost always die first and the youngest leaves are the last to die. Shaded leaves often die from desiccation resulting from loss of water to exposed leaves and branches during periods of stress. Shaded leaves probably develop a lower maximum diffusion-

pressure deficit because reduced photosynthesis in the shade results in a lower concentration of carbohydrates. Because the roots have a relatively low osmotic pressure, they presumably suffer from competition among the various tissues for water.

It has been well established that when an internal water deficit develops water usually moves from fruits to leaves, with a resultant decrease in the rate of growth of the fruits. This often is demonstrated by placing under similar conditions cut branches with and without fruits, when it is found that the leaves remain unwilted much longer on the branch bearing fruits than on the branch without fruits. Bartholomew (1926) observed that lemon fruits growing on trees in moist soil began to shrink about 6 A.M. and continued to shrink until about 4 P.M., which would indicate that water loss exceeds absorption during this period. From 4 P.M. to 6 A.M., the fruit increased in size. The amount of shrinkage was greater on trees in dry soil, but it occurred even when no perceptible wilting of leaves could be detected. When transpiration was very rapid for an extended period of time, there was not only a daily water deficit, but also one lasting over a period of 3 or 4 weeks, which seriously affected the size and quality of the fruit. Hendrickson and Veihmeyer (1941b) reported that Bartlett pears increased in size from 6 P.M. until 8 A.M., after which they decreased slightly during the day. Decreased growth rates occur in apples when water deficits are developed in the trees (Magness, Degman, and Furr, 1935), and this probably is true of most fruits (see Figs. 46 and 47). It appears that green fruits generally do not develop diffusion-pressure deficits as large as those developed in leaves.

The situation has been somewhat oversimplified thus far by assuming that the diffusion-pressure deficit of a tissue is determined solely by the osmotic pressure of the cell sap, plus any tension applied in excess of this value. There is evidence that certain tissues—mostly young, growing ones—can develop diffusion-pressure deficits in excess of the os-

motic pressure of their expressed sap. As was mentioned in Chap. 8, this has been taken by some observers to indicate the existence of a nonosmotic or secretory mechanism which causes water intake by cells, but it may result from an excess of imbibitional forces over osmotic forces in certain tissues. Anderson and Kerr (1943) found that fully grown cotton
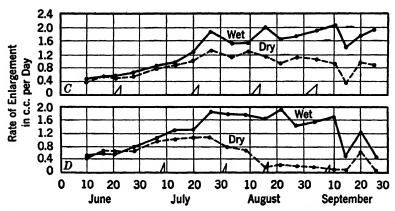
FIG. 46. Effect of soil moisture supply on rate of enlargement of pears. The wet plots were irrigated on the dates indicated by the triangles on the abscissas, water being applied whenever fruit growth began to slow down. *C* shows results on adobe clay; *D*, results on sandy loam. Fruit growth was retarded more on dry plots on the sandy soil, because it held less available water per unit of volume. (*From Ryall and Aldrich, 1944.*)

bolls shrink when the plants on which they are growing wilt, but that they regain full size during the night if soil moisture is not limiting. When the soil is very dry, the daily period of shrinkage is longer, and recovery at night either is only partial or else fails to occur. They also observed that plants bearing numerous fully grown bolls wilted less than plants with young bolls did, probably because the older bolls served as water reservoirs. The enlargement of young bolls is not prevented by even very severe wilting of the plants. Apparently young bolls, unlike mature ones, can absorb water from wilted plants. Possibly this is because the high imbibitional forces of the slightly vacuolated young cells result

in development of much higher diffusion-pressure deficits than would be expected from the osmotic pressure of their sap. Stocking (1945) reported instances where young, apical leaves of squash remained unwilted, although their diffusion-pressure deficit appeared to be lower than that of the wilted older leaves. It appears that under some circumstances, particularly in actively growing plant tissues, the force with which water actually can be absorbed is not indicated reliably by conventional methods of measuring diffusion-pressure deficit.

Effects of Internal Water Deficits on Plants

Many studies of anatomical, morphological, and biochemical changes, and of changes in rates of physiological processes caused by lack of water have been published. Since detailed consideration of these phenomena is more closely related to the realm of drought effects than to the absorption of water, they will not be considered in detail in this book and the reader is referred to Crafts, Currier, and Stocking (1948), Maximov (1929), and Miller (1938) for more detailed discussions and for additional references. A few examples of the more interesting effects are discussed in the following pages.

Effects of Internal Water Deficit on Growth. Everyone is familiar with the stunted plants produced under drought conditions. This stunting represents both the direct and the indirect effects of severe and long-continued internal water deficits. Among the important direct effects is reduction in cell division and in cell enlargement. These effects are reflected in the frequently observed fact that plants often elongate more at night than during the day. Such behavior has been observed in many species, including bamboo, corn, date palms, and pine trees (Miller, 1938). It also has been observed that sometimes growth ceases or the stems even shrink during the middle of the day but recover and elongate further during the night. This tendency is most noticeable on bright sunny days when transpiration is high;

whereas in warm, cloudy weather growth during the day frequently exceeds growth during the night. Loomis (1934) concluded that the growth of maize depends primarily on an adequate supply of water at the growing tip. This is limited most frequently by excessive transpiration, the restricted
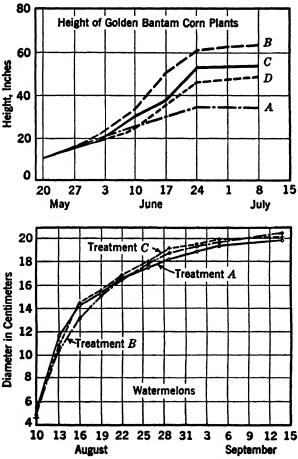
FIG. 47. Effects of irrigation on height growth of sweet corn (shallow-rooted), and watermelon (deep-rooted) on a clay-loam soil at Davis, California. Treatments: *A*, no irrigation; *B*, eight irrigations; *C*, three irrigations; *D*, two irrigations. The yield of watermelons was practically as good on the unirrigated plots as on the irrigated plots, but the growth and yield of corn were seriously reduced by lack of water. (*From Doneen and MacGillivray, 1948.*)

absorption caused by dry soil being second in importance as a limiting factor. Reed (1939) found that seedlings of *Pinus taeda* and *P. echinata* made nearly twice as much height growth at night as during the day in late June and early July. He believed this was because transpiration was lower during the night and less water deficit existed in the growing regions.

Thut and Loomis (1944) found that elongation of stems and enlargement of leaves of several species of plants were materially reduced by internal water deficits. As the greatest water deficit occurs near midday, and as growth at night is often limited by low temperatures, maximum growth commonly occurs in the early morning and again in the evening, with a distinct reduction near midday. MacDougal (1920) observed that the youngest part of growing sunflower stems continued to increase in diameter, while the older part was shrinking because of loss of turgor by the cells. Wilson (1948) found that tomato stem tips continue to elongate even when the part of the stem below the first node shows shrinkage caused by dehydration. The observation of Anderson and Kerr (1943) that young cotton bolls continue to enlarge, even when the plant bearing them wilts, also suggests that actively growing tissues can absorb water from more mature tissues, even when the latter have lost their turgor. The apparent midday cessation of enlargement may be largely the result of shrinkage of mature cells, and enlargement may continue in the growing regions even while the older cells are losing their turgidity and are shrinking. Huber (1937) cites work indicating that water deficit interferes with cell division, particularly reductional division. Numerous observations have shown that midday shrinkage in diameter of tree trunks is a common occurrence when transpiration is rapid. This is caused by loss of turgor of the living cells and by development of tension or negative pressure which causes contraction of the nonliving xylem elements (MacDougal, 1938, Chap. III).

The anatomical differences between sun and shade leaves

probably are at least partly the result of differences in tur-
gidity of cells. The frequent loss of turgidity by leaves that
are growing in full sun probably checks cell enlargement and
results in reduced leaf area and differences in anatomy, as
compared with shade leaves, which are seldom wilted. It
appears probable, however, that not all xeromorphic leaves
are the result of water deficits. The xeromorphic leaf struc-
ture of many species growing in bogs has long been attrib-
uted to "physiological drought," but this is questioned by
Caughey (1945). Perhaps it is partly related to the nutri-
tion of the plants (Albrecht, 1940; Mothes, 1932).

Effects of Water deficit on Stomatal Opening. Appar-
ently the stomates are very sensitive to a water deficit in the
leaves. According to Magness, Degman, and Furr (1935),
a reduced period of stomatal opening is the first measurable
effect of reduced moisture supply to apple trees. By follow-
ing stomatal behavior throughout the day it is possible to
detect variations from normal while the moisture content of
the entire root zone is still considerably above the wilting
percentage. Stomatal closure is very closely correlated with
decreased moisture content of the leaves; the earlier in the
day a moisture deficit develops, the earlier the stomates close
(see Fig. 48). Jones (1931) found that the stomates of
peaches growing in dry soil were open for a shorter period
each day than were those of peaches growing in moist soil.
Yocum (1935) observed that the stomates of oak seedlings
growing in dry soil were closed during the day although
those on well-watered seedlings were open. While excep-
tions exist, in general stomates tend to close during the day,
when an excess of water loss over absorption causes a mois-
ture deficit in the leaves. Maximov and Zernova (1936)
concluded from studies with irrigated and unirrigated wheat
that the extent of opening of stomates during the day may
serve as a good indication of the amount of water available
to the plants. Oppenheimer and Elze (1941) also concluded
that the stomatal aperture of citrus leaves is a reliable indi-
cator of whether or not irrigation is needed, because as the

soil dries, the stomates close progressively earlier in the day. Figure 48 shows the effect of increasing water deficit on the behavior of pear stomates.
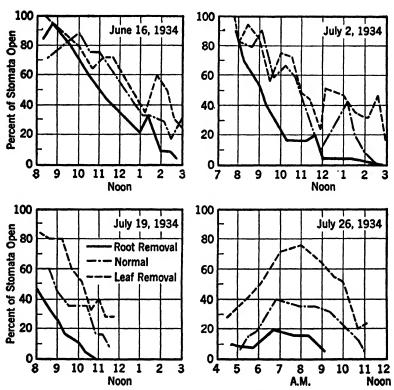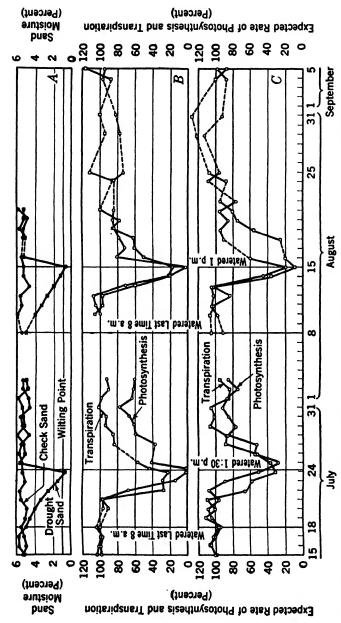
FIG. 48. Effects of moisture deficit on daily closure of stomates of pear. As the season progressed and available soil moisture decreased, the stomates closed earlier in the day. Those on trees with one-fifth of the roots removed closed earlier than those on trees with one-fifth of the leaves removed, because the former developed an internal water deficit earlier in the day. (*From Aldrich and Work, 1934.*)

Effects of Water Deficit on Photosynthesis. A water deficit in the leaves seriously reduces the rate of photosynthesis. Potted apple trees that were allowed to deplete gradually the available soil moisture showed over 50 per cent reduction in photosynthesis before any wilting was evident. After wilting became visible, photosynthesis was reduced to

only 15 per cent of the expected rate (Schneider and Childers, 1941). Respiration increased materially as the moisture stress increased. Decreasing soil moisture also causes decreased photosynthesis in pecan trees, the amount of reduction being greatest when conditions are favorable for high transpiration (Loustalot, 1945). This is shown in Fig. 49. Photosynthesis increased rapidly when the soil was wetted but did not return to normal for several days. Kozlowski (1947) found that the rate of photosynthesis of potted pine seedlings decreased as the soil was allowed to dry out and practically ceased at the permanent-wilting percentage. Photosynthesis was also reduced in Eastern red oak, but less rapidly than in pine.

This reduction in photosynthesis may be in part a direct result of dehydration of the protoplasm of the leaves, and it may be in part the result of closure of stomates. It has been demonstrated by various workers that low leaf-moisture content will, in itself, reduce photosynthesis (Rabinowitch, 1945). Closure of stomates also ought to reduce it by cutting off the supply of carbon dioxide, but some difference of opinion exists concerning the effects of stomatal closure on photosynthesis. Yocum (1935) found that closure of stomates of oak seedlings growing in dry soil was accompanied by complete disappearance of starch from the leaves. Heinicke and Childers (1937) observed that photosynthesis was reduced only 25 per cent, while transpiration was reduced 50 per cent in an apple tree growing in dry soil. Mitchell (1936) reported that tomato and Pelargonium plants continued to absorb carbon dioxide even when the stomates appeared to be closed. Nutman (1937), in contrast, observed that the midday closure of stomates characteristic of coffee trees was invariably accompanied by a marked decrease in photosynthesis. Schneider and Childers (1941) observed fairly high rates of photosynthesis in apple on several occasions when the stomates appeared to be closed. Freeland (1948) found that, although most of the carbon dioxide enters leaves through the stomates, in some species it enters

FIG. 49.   Effects of decreasing soil moisture on photosynthesis and transpiration of pecan seedlings growing in sand: *A*, moisture content of sand; *B*, rates of photosynthesis and transpiration during the afternoon, expressed as percentages of the rates expected with well-watered plants; *C*, similar rates during the forenoon.   Effects of dry soil were greater in the afternoon, because more rapid transpiration caused a greater water deficit in the leaves in the afternoon.   (*From Loustalot, 1945.*)

rather rapidly even when the stomates appear to be closed. Whether or not photosynthesis is seriously reduced by stomatal closure probably depends on the permeability of the epidermis to carbon dioxide.

Biochemical Effects of Water Deficit

The chemical composition of plants can be materially modified by internal water deficits. One of the most common effects is the conversion of starch to sugar. Magness, Regeimbal, and Degman (1933) reported that moisture deficiency decreases the starch reserves in apple trees. Spoehr and Milner (1939) found that the wilting of leaves is accompanied by the conversion of starch to sugar. Wadleigh and Ayers (1945) found a low starch content in bean plants which were subjected to a high soil-moisture tension, but no difference in reducing sugar content compared to plants grown with a low soil-moisture tension. Eaton and Ergle (1948) reported that drought caused a decrease in the starch content and an increase in hexose-sugar content of cotton leaves, but a large increase in starch, hexoses, and sucrose in the stems and roots. They concluded that this accumulation occurred because drought decreases the use of carbohydrates more than it decreases photosynthesis in cotton.

Vassiliev and Vassiliev (1936) found that, in general, wheat plants exposed to drought differ from well-watered plants by being higher in hemicellulose and sugars, especially sucrose. Clements (1937) reported that, under drought conditions, soybeans produce large amounts of hemicellulose and that starch is present in larger amounts than in well-watered plants. Nightingale and Mitchell (1934) reported that tomato plants subjected to very high humidity for 9 days grew more rapidly and accumulated less carbohydrate than did plants grown with low humidity. High moisture stress caused by low humidity caused an increase in nitrate nitrogen and a smaller increase in soluble organic nitrogen. It was suggested by Nightingale and Farnham (1936) that a water deficit interferes with protein synthesis,

but according to Wadleigh and Ayers (1945), this view is not supported by work at the U.S. Regional Salinity Laboratory. Clements (1937) also reported a high level of nitrogen metabolism in plants that were grown with deficient soil moisture. Evidently plants of different species react differently to high moisture stress.

Fruit grown under moderate moisture stress often differs somewhat in texture and composition from that grown with an abundance of water. Ryall and Aldrich (1944) found that pears from dry plots were sweeter in taste and firmer than those from wet plots, but pears from wet plots were somewhat more mellow. Increased moisture stress decreases the amount of growth made by guayule, whether it is produced by means of a high concentration of salt or by allowing the soil to dry out. The relation of rubber content to moisture stress is not so simple, however. Although a moderate increase in moisture stress increases the rubber content, a high moisture stress greatly decreases it (Wadleigh, Gauch, and Magistad, 1946). This is shown in Fig. 50.

Effects of Water Deficit on Permeability of Roots

Plants which have been permanently wilted often recover very slowly after the soil is watered. Although the leaves may regain their turgidity in a few hours, the rates of transpiration and photosynthesis may not return to normal for several days (Loustalot, 1945). The author has unpublished data indicating that considerably less water will pass through the roots of wilted plants under a given pressure gradient than will pass through the roots of similar plants that have not been wilted. This decrease in water intake might be the result of decreased permeability or of decreased absorbing surface. Perhaps the time required for recovery represents the time required for the resumption of root elongation, but Woodroof and Woodroof (1934) state that pecan roots resume elongation within 24 hours after the soil is wetted. The effects of moisture stress on root growth and functioning deserve further study.
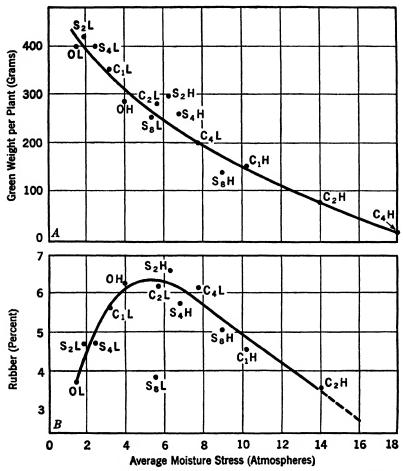
FIG. 50. Relation of average moisture stress developed during irrigation intervals and (A) the growth of guayule plants, and (B) the percentage of rubber in the millable bush. (*From Wadleigh, Gauch, and Magistad, 1946.*) The symbols refer to various treatments as follows:

O = No salt added	S_2 = 0.2% Na_2SO_4 added
C_1 = 0.1% NaCl added	S_4 = 0.4% Na_2SO_4 added
C_2 = 0.2% NaCl added	S_8 = 0.8% Na_2SO_4 added
C_4 = 0.4% NaCl added	

L = Low tension. Water added to bring soil back to field capacity when tension of 300 to 400 cm. of water was indicated by tensiometers.

H = High tension. Water added when average moisture content fell to permanent-wilting percentage.

Beneficial Effects of Water Deficit

Under some circumstances, moderate moisture stress may be beneficial even though it reduces vegetative growth somewhat. Plants grown under conditions of an abundance of soil moisture and high humidity often are very succulent and have a low proportion of roots to shoots; hence they suffer more injury from desiccation when they are transplanted or exposed to dry air than would plants grown under moderate moisture stress. According to Jones (1944), the disease known as onion blast occurs when onions grown during a period of cloudy, wet weather are suddenly exposed to bright sun, high temperatures, and low humidity. The combination of a large top and small root system results in quick dehydration and injury when transpiration becomes rapid. Watering of greenhouse crops is reduced during cloudy, cool weather to prevent too succulent growth, which often is more susceptible to disease and less productive than is the "hard" growth obtained with less water. Kelley, Hunter, and Hobbs (1945) found that guayule plants grown under high moisture stress resumed growth sooner after transplanting and survived better than did plants that were grown with low moisture stress. Seedlings of herbaceous species often are "hardened" by reducing the water supply so that they will survive transplanting better.

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